PATTERN, NUMBER, VARIABILITY, AND TAXONOMIC SIGNIFICANCE OF INTEGUMENTAL ORGANS (SENSILLA AND GLANDULAR PORES) IN THE GENUS *EUCALANUS* (COPEPODA, CALANOIDA)

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ABSTRACT

Methods for study of bilaterally symmetrical, serially homologous sets of integumental organs comprising hair, peg, and pit sensilla and the pores of integumental glands as well as their number and distribution in the genus *Eucalanus* are described.

A survey of these organs was carried out on geographically representative samples of the 17 discrete populations I recognize as valid species in the genus. The survey concentrated on adult females, but smaller numbers of adult males and some younger copepodid stages were also examined. Numbers and arrangement of these organs, estimates of variability, and their relationship to total length were established for each species. Phenetic similarity in integumental organ arrangement is shown to concur with other morphological features within the genus. Comparison is also made between number and arrangement of integumental organs and the geographical relationships among the members in each species group. Several new species in the attenuatus group are described on the basis of integumental organs and geographical distribution. A preliminary study of geographical variation in the circumglobal, broadly tropical species *E. subtenuis* is used to estimate the general complexity of genetic control and the use of these organs to study gene flow and population variability in planktonic species.

The integument of arthropods bears numerous organs that fall into two general classes: sensory receptors or sensilla, and glands. Sensilla are composed of one to several sensory neurons and generally two accessory cells, the latter forming the external features which may be in the form of an outgrowth, i.e., a hair, a cone, or a peg, or an ingrowth such as a pit or plate organ with sensory cell bodies located underneath (Laverack, 1969; Schneider, 1969; Stürckow, 1970). The regular presence of sensilla containing nerve fibers has been demonstrated histologically in a variety of different copepods (e.g., Fahrenbach, 1962; Elofsson, 1971).

In terrestrial arthropods integumental glands are highly variable in number, in distribution, and in morphological detail (Eisner and Meinwald, 1966). Integumental glands described from copepods tend to be rather simple sacs underlying the integument and communicate with the environment via a simple pore penetrating the integument (e.g., Clarke et al., 1962; Fahrenbach, 1962; Park, 1966).

On the body of copepods as in mystacocarids and other arthropods, sensilla and glands are in general distributed in bilaterally symmetrical patterns that are somewhat redundant on successive body segments, i.e., they appear to be serially homologous (Sewell, 1929, 1932, 1947; Fahrenbach, 1962; Hessler, 1969). It is highly probable that chemical communication via integumental organs, a widespread means for exchanging information among arthropods and vertebrates (e.g., cf. Johnston, Moulton, and Turk, 1970) is essential to copepods. Dioecious and nonparthenogenetic copepods must locate and correctly identify a potential mate without visual aids. This search and contact procedure is mediated by pheromones in *Eurytemora* and called "mate-seeking behavior" (Katona, 1973). Moreover successful culmination of the mating act requires attachment of the spermatophore

that permits passage of the sperm into the female's seminal receptacles (Wolf, 1905; Neubaur, 1913; Heberer, 1932; Fahrenbach, 1962).

Integumental organ systems are used widely in arthropod systematics. Indeed, in some groups, as for example, mosquitoes, dependence upon chaetotaxy is essential. A unique and particularly interesting application devised to permit identification of the fossilized remains of chydorid cladocerans in extinct lake sediments utilizes the number, size, and arrangement of integumental pores (Frey, 1959, 1962).

Despite repeated mention of integumental organs in the early copepod literature, attempts to apply them to study of marine species are rare. Notable exceptions must include With's (1915) detailed accounts of the sensilla surrounding the oral region for a number of species collected in North Atlantic samples. Sewell showed considerable interest in the general distribution of body integumental organs in planktonic copepods. His observations made on a broad variety of species are presented in scattered notes, remarks, and illustrations within the context of his faunal studies on Indian Ocean calanoids (1929, 1932, 1947). Unfortunately, the diminutiveness of these organs, Sewell's omission of methods for study, and a critical estimate of their reliability contributed to their neglect by subsequent workers. Two studies on bioluminescence in planktonic copepods (David and Conover, 1961; Clarke et al., 1962) call attention to the potential value of luminescing integumental glands for identifying the species of living specimens.

Conventional taxonomic systems organizing diversity among calanoid copepods are strongly dependent upon sexually modified structures of the adult (copepodid stage VI) sometimes assisted by nonsexual morphological or meristic features in the adult condition, as for example, spination and setation of appendages, segmentation of appendages, and segmentation of body tagmata. These sources of diagnostic information serve all hierarchial levels, species to family. Due to the nature of calanoid ontogeny, all of these structures assume their definitive state only in sexually mature adults. Thus, juveniles lie outside of existing systems, males and females are only rarely served by the same

system, and genera that are relatively undistinguished in sexually modified structures tend to be "taxonomically difficult."

The primary purpose of this paper is to demonstrate the potential significance of sensilla and the pores of integumental glands on the body tagmata to the systematics and phylogeny of calanoid copepods. From a survey of these organs in the genus *Eucalanus*, their numbers and arrangements provide an objective basis for grouping related species, for distinguishing between sibling species, for relating adults of either sex to their respective species despite the elimination of other common characters by sexual dimorphism, for aiding in the specific identification of late immature copepods, and for the determination of regionalized cohorts that apparently lack unrestricted gene flow with morphologically similar cohorts in other regions.

REMARKS ON THE GENUS *EUCALANUS* DANA, 1853

Eucalanus is a universally familiar marine genus of eucalanid copepods. It contains primary consumers that form a conspicuous part of the epiplanktonic and uper mesoplankton in low to middle latitudes; some of the species are primarily oceanic, others are neritic. Within its habitat many of the species tend to be among the most abundant and largest (adult total length ranges from about 3 to 7 mm) of the regional copepod fauna. Since the inception of the genus for *E. attenuatus* (Dana, 1853), about 25 nominal species have been proposed. Contributions by Giesbrecht (1892), Johnson (1938), and Vervoort (1946, 1963) provide the framework for the genus and its taxa. The current world literature indicates 12 nominal species in active use. Two are represented by two subspecies each, yielding a total of 14 widely accepted taxa.

Though *Eucalanus* is a morphologically distinctive genus and its species are widespread and relatively abundant, frequent questions and confusion about the validity and rank of its nominal species and subspecies tarnish its literature. Difficulties with the identification

of the species emanate largely from the absence of distinctive sexually modified appendages, the few available meristic characters in setation and the widespread dependence of the existing taxonomic system upon relatively subtle shapes and proportions of segments and tagmata unsupported by rigorous estimates of variability. Difficulties and inconsistencies associated with the rank of the taxa in the genus *Eucalanus*, notably in the elongatus group, might be the product of several factors: e.g., the lack of accurate data on geographical distribution, uncertainties about the significance of morphological differences among the subspecies, the widespread lack of an adequate basis for viewing the planktonic taxon in the perspective of a biological population.

For example, questions or expressed doubts challenge the validity of separating *E. pileatus* from *subcrassus*, and the two have often been confused with *monachus* (Deevey, 1960; Grice, 1962; Vervoort, 1963; Lang, 1965). Confusion about *subtenuis* appears to trouble some (Fukase, 1957). Awareness of variation and taxonomic complexity within the nominal species *attenuatus* has been noted frequently (Sewell, 1947; Tanaka, 1956; Brodsky, 1962; Lang, 1965; Park, 1968), and similar questions must be raised regarding *dentatus* (Fleminger, unpublished data). Finally, a point must be made with regard to the elongatus complex. Three decades have passed since Johnson's (1938) perspicacious revision based on so few data, decades of increasing oceanographic activity and the accumulation of geographical and morphological observation on these common forms. Considering our increased experiences and understanding the logic of justification for the general practice of regarding *inermis* as a full species but continuing the two subspecies of *elongatus* and the two subspecies of *bungii* escapes me. On the basis of both morphology and geography the known similarities and differences between *inermis* and its two cognates and those between the subspecies of each of these cognates are about equal.

As part of an unpublished doctoral dissertation, Lang (1965) presented a taxonomic review and study of the distribution of *Eucalanus* in the Pacific Ocean based on plankton samples from the Scripps Institution of Oceanography Zooplankton Collections. Lang's data on the elongatus complex, published in 1967, contributed appreciably to our knowledge of geographical relationships among its populations. Though providing considerable evidence favoring extension of the revision initiated by Johnson (1938), his use of subspecies was retained. Expressed dissatisfaction with separation of *pileatus* and *subcrassus* and the considerable variation encountered in *attenuatus* s.l. were noted in the unpublished portion of Lang's dissertation.

My attempts to strengthen the *Eucalanus* section of Lang's manuscript for publication using the material on hand to clarify unresolved issues were unsuccessful. Two issues emerged: Resolution of the difficulties depended on 1) expanding geographical representation to encompass the world ocean and 2) the need to develop more reliable morphological characters for distinguishing the reproductively isolated populations within the genus. As conditions permitted, I gathered geographic records and specimens of *Eucalanus* in conjunction with global studies on other calanoid genera including *Clausocalanus* and *Pontellina* (Frost and Fleminger, 1968; Fleminger and Hulsemann, in press). In addition, I began to examine various structures of *Eucalanus* at relatively high magnifications ($200\times$ to $600\times$). Useful characters were found in the female genital segment, especially in the shape and arrangement of the seminal receptacles, and in the male fifth legs. For example, general similarities in the seminal receptacles provided a promising basis for phylogenetic groupings within the genus and a dependable means for separating at least some of the species of the pileatus group (Figure 1).

In the course of my survey, distinctive patterns in the distribution of integumental organs on the urosome became apparent. Recall of Sewell's (1947) use of these features to support his separation of *attenuatus* and *pseudattenuatus* prompted development of procedures described below to map integumental organs on dorsal and lateral surfaces of all body segments. The results provided the means for separating regional populations, species, and species
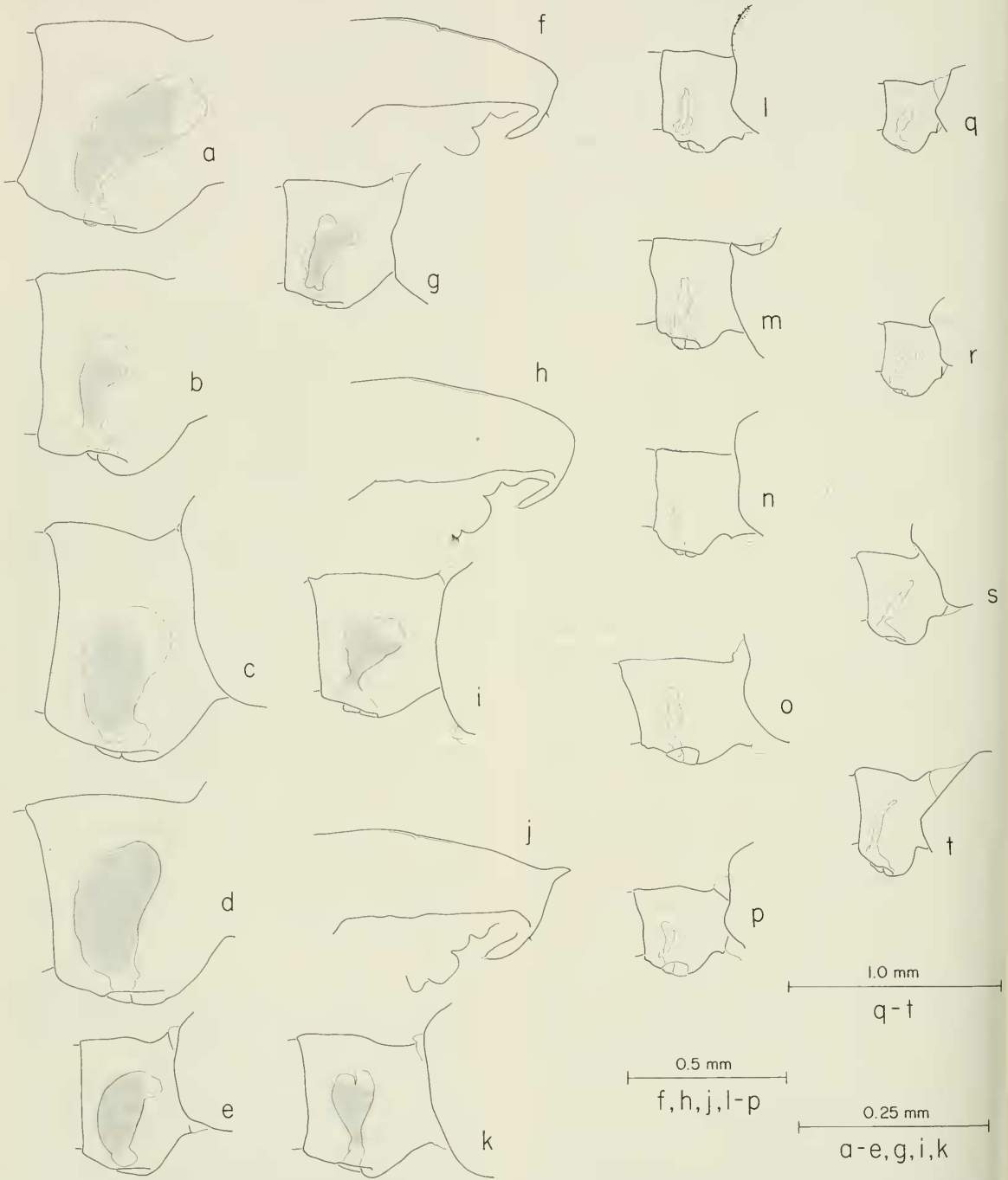
1.0 mm
q-t

0.5 mm
f,h,j,l-p

0.25 mm
a-e,g,i,k

FIGURE 1.—Genus *Eucalanus*. Genital segment, lateral view, female—**a.** *subtenuis* (Downwind 28); **b.** *mucronatus* (Monsoon 11); **c.** *crassus* (Alaska 4-36); **d.** *longiceps* (Monsoon 24); **e.** *monachus* (Alaska 5-7); **g.** *pileatus* (Lusiad VII Freetown); **i.** *subcrassus* (Lusiad 11 H-1); **k.** *dentatus* (Naga S11A 61-198); **l.** *elongatus* (Naga S11A 61-127); **m.** *hyalinus* (TRANSPAC 10 B); **n.** *inermis* (Muddauber 137-1); **o.** *bungii* (TRANSPAC 65 B); **p.** *californicus* (5606 50.80); **q.** *attenuatus* (EASTROPAC A 207); **r.** *sewelli* (Atlantis 11-31-119); **s.** *parki* (Boreas 19); **t.** *langae* (Monsson 24). Anterior portion of head, lateral view, female—**f.** *pileatus* (Lusiad VII Freetown); **h.** *subcrassus* (Lusiad 11 H-1); **j.** *dentatus* (Naga 61-198). The shaded areas indicate the extent of sperm in the seminal receptacle. Positions for stations mentioned are listed in Snyder and Fleminger (1965, 1972).

groups within the genus and concurred with the evidence derived from study of the seminal receptacles. Greater appreciation of the reproductively isolated populations within *Eucalanus* (Table 1) also revealed the compelling need for much additional work on finer details to complete a satisfactory account of each species. The four geographical forms of *attenuatus* s.l. require comparative study of conventional morphological features in both sexes. Their geographical distributions should be amplified by reexamination of the great number of records and sorted specimens now in hand recorded collectively under *attenuatus* s.l.

Evidence of geographical variation in *subtenuis*, described below, requires additional study and should be examined in the context of co-occurrence with its sibling congener, *mucronatus*. Also, closer geographical scrutiny should be made of other widely ranging species showing broadly neritic habitat preferences such as *crassus* and *pileatus*.

Realization that the significance of integumental organs in copepods overshadows and holds more widespread interest than the genus *Eucalanus* is the basis for presenting the survey of sensilla and pores within the framework of an incomplete taxonomic review. Completing the global account of *Eucalanus* first would impose a long and unnecessary delay. Based on seminal receptacles, geography, and integumental organs, the essential diversity within the genus is now unmistakably clear. Details still

TABLE 1.—Author's provisional list of valid species and phylogenetic groupings comprising the genus *Eucalanus*. Summarized distribution and biogeographic assignment based on records confirmed by author.

subtenuis group:
1. *E. subtenuis* Giesbrecht, 1888. Broadly Tropical, circumglobal[1] in eutrophic oceanic waters; epiplanktonic. Figure 9e.
2. *E. mucronatus* Giesbrecht, 1888. Tropical, Indian Ocean to western Pacific in equatorial circulation systems[2]; epiplanktonic. Figure 9d.
3. *E. crassus* Giesbrecht, 1888. Tropical-subtropical, circumglobal in eutrophic broadly neritic waters; epiplanktonic. Figure 9a.
4. *E. longiceps* Matthews, 1925. Boreal-temperate, circumglobal, Southern Hemisphere West Wind Drift system (= Southern Ocean Transition zone); epiplanktonic? Figure 9b.
5. *E. monachus* Giesbrecht, 1888. Tropical-subtropical, Atlantic, broadly neritic; subsurface epiplanktonic. Figure 9c.

pileatus group:
6. *E. pileatus* Giesbrecht, 1888. Tropical-subtropical, circumglobal, coastal- neritic; epiplanktonic. Figure 11a.
7. *E. subcrassus* Giesbrecht, 1888. Tropical, Indo-Pacific, broadly neritic; epiplanktonic. Figure 11c.
8. *E. dentatus* Scott, 1909. Tropical, Austral-Asian seas; coastal epiplanktonic. Figure 11b.

elongatus group:
9. *E. elongatus* (Dana, 1849). Tropical, Indian Ocean to western Pacific in equatorial circulations; epiplanktonic? Figure 13b.
10. *E. hyalinus* (Claus, 1866). Tropical-subtropical, circumglobal especially in eutrophic, oxygenated waters adjacent to boundary currents; deep epiplankton to upper mesoplankton. Figure 13c.
11. *E. inermis* Giesbrecht, 1892. Eastern Tropical Pacific in eutrophic, low oxygen water; deep epiplankton to upper mesoplankton. Figure 13a.
12. *E. bungii* Giesbrecht, 1892. Boreal-subpolar, North Pacific, and Bering Sea; epiplanktonic to upper mesoplanktonic.
13 *E. californicus* Johnson, 1938. Temperate, North Pacific, West Wind Drift system (= North Pacific Transition zone); deep epiplanktonic to upper mesoplanktonic. Figure 13d.

attenuatus group:
14. *attenuatus* (Dana, 1849). Tropical, Indo-Pacific equatorial circulation systems; epiplanktonic. Figure 15d.
15. *sewelli* sp.n. Tropical-subtropical, circumglobal; epiplanktonic. Figure 15c.
16. *parki* sp.n. Temperate, North Pacific, West Wind Drift system (= North Pacific Transition zone); deep epiplanktonic to upper mesoplanktonic. Figure 15a.
17. *langae* sp.n. Temperate, circumglobal, Southern Ocean West Wind Drift system (= Southern Ocean Transition zone); deep epiplanktonic and upper mesoplanktonic. Figure 15b.

[1] Evidence of three regionalized populations: Eastern Tropical Pacific; Tropical Indian Ocean to western Tropical Pacific; Tropical Atlantic.
[2] Two questionable records from Tropical Atlantic: Florida Current (Owre and Foyo, 1967) and Gulf of Mexico (Fleminger, unpublished data). Forehead pointed but basal segment of mondible with two setoe.

TABLE 2.—Adult female *Eucalanus*: collecting localities and numbers of specimens surveyed for sensilla and pores. All samples taken with open nets ½ m or larger in diameter at the mouth and towed horizontally or obliquely at epiplanktonic depths.

Cruise or ship	Station	Latitude	Longitude	Date	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
Afram[1]	F-1	14°00'N	17°30'W	?			5		2												
Alaska[2]	4-36	23°31'N	86°44'W	24 Jan 52	2																
	5-9	26°00'N	87°32'W	26 May 52																2	
	11-5	29°07'N	88°47'W	30 May 53					3	2											
Arctic Exped.	1310(4)	38°49'N	168°03'W	19 Jul 47												5					
Atlantis II-31[3]	15	24°42'N	49°42'W	19 Jan 67															1		
	31	20°07'N	20°36'W	27 Jan 67			3														
	33	19°21'N	16°52'W	28 Jan 67					3												
	34	18°35'N	16°59'W	28 Jan 67	4		2				2										
	35	17°54'N	17°20'W	28 Jan 67			5														
	36	15°45'N	17°45'W	29 Jan 67					7												
	43	08°08'N	19°48'W	9 Feb 67					5											7	
	45	05°41'N	21°29'W	11 Feb 67																1	
	46	04°09'N	22°45'W	11 Feb 67										1						1	
	48	00°56'N	25°20'W	12 Feb 67					2												
	51	00°07'N	28°43'W	14 Feb 67					2												
	74	29°11'S	40°06'W	12 Mar 67																3	
	80	26°20'S	46°05'W	28 Mar 67																2	
	119	30°23'N	64°17'W	30 Apr 67																1	
	122	35°12'N	67°15'W	2 May 67																2	
	123	36°59'N	68°50'W	2 May 67										3							
Azul I	F-1	23°38'N	109°36'W	5 Sep 62					4												
Boreas	19	41°57'N	165°06'W	2 Feb 66													1	2			
	64	58°21'N	168°57'E	15 Feb 66												5					
	148	48°55'N	157°55'E	12 Mar 66												4					
Bureau of	F1832	34°02'S	17°44'E	8 May 62					1										1		
Sea Fisheries[4]	A2000	33°04'S	17°16'E	8 Sep 62										3							
	A2003	33°05'S	17°47'E	8 Sep 62					1												
	90.28D	33°28'N	117°47'W	13 Jun 52												3					
CalCOFI 5206	120.50	27°33'N	115°52'W	18 Apr 55												5					
5504	144G.15	24°28'N	110°28'W	24 Aug 57																2	
5708	137.30	25°20'N	112°45'W	10 Jul 58									2								
5807	PT 18	22°31'N	105°53'W	26 Aug 61							5		5								
6108	27	03°30'S	121°54'W	9 Feb 53					2												
Capricorn	31	06°31'S	124°41'W	13 Feb 53																	3
	32	07°58'S	124° 11'W	14 Feb 53									1								
	5	15°41'N	64°12'W	14 Jun 65					2												
Chain 49[3]	9	19°52'N	69°57'W	16 Jun 65					7												
	13	14°48'N	68°09'W	26 May 66																1	
Chain 60[3]	15	12°58'N	73°34'W	28 May 66		5															
	4	42°33'N	162°09'W	17 Jul 56											1			4			
Chinook	8	40°28'N	173°04'W	3 Aug 56											2			4			
	NT 3	22°28'N	177°21'E	5 Apr 68					1												
Circe	NT 8	17°29'N	141°38'E	16 Apr 68					1												
	NT 11	05°11'N	123°58'E	20 Apr 68																1	1
	NT 14	08°28'N	118°24'E	23 Apr 68				5						2							
	NT 15	07°16'N	115°20'E	24 Apr 68					4												
	NT 16	05°39'N	112°39'E	25 Apr 68										2							
	NT 25	19°04'N	87°47'E	17 May 68																	1
	NT 27	09°46'N	83°31'E	23 May 68																	2
	NT 30	07°27'N	77°42'E	28 May 68															4		
	NT 33	19°42'S	63°12'E	28 Aug 68					2												
	Camera 3	26°28'S	46°04'E	29 Sep 68					1												
	Dm 2.75.63	11°00'S	110°00'E	26 May 63								2									
Diamantina[5]	36	06°05'N	49°53'E	16 Aug 64																	3
Dodo VI	49	10°19'N	53°11'E	20 Aug 64								2									
	54	10°23'N	51°43'E	22 Aug 64	2																
	55	10°14'N	51°19'E	22 Aug 64			4							5							
	55-15	09°45'N	51°31'E	23 Aug 64					1											1	
	60	11°58'N	55°11'E	26 Aug 64					2	1		7		1						2	
	86	12°00'S	55°55'E	5 Sep 64								5									
Downwind	19B	46°25'S	123°38'W	4 Dec 57	7																
	20C	44°36'S	112°08'W	10 Dec 57														1			
	22A	40°39'S	92°02'W	17 Dec 57														1			
	24	34°30'S	79°30'W	20 Dec 57																2	
	28	27°08'S	72°02'W	31 Dec 57					3			3								3	
EASTROPAC	J 087	01°34'N	105°00'W	26 Feb 67					3												
	A 207	13°23'S	126°00'W	19 Feb 67					3												3
Eastropic	82	08°00'N	104°00'W	9 Dec 55								6									

TABLE 2.—*Continued*

Cruise or ship	Station	Latitude	Longitude	Date	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
El Golfo I	I CN2	24°38'N	109°22'W	14 Nov 63									2								
	II CD1	25°35'N	110°14'W	17 Nov 63									1								
	VI AN2	28°37'N	112°56'W	25 Nov 63																1	
El Golfo II	XIV B2D1	26°31'N	111°03'W	22 May 65																1	
EQUAPAC	H 20	10°00'S	163°00'E	17 Aug 56																	3
	S 1	20°43'N	158°27'W	21 Aug 56					5												
	S 20	00°51'N	167°14'W	29 Aug 56						10											
	S 21	00°02'N	166°59'W	29 Aug 56																	1
	S 23	01°55'S	166°52'W	30 Aug 56																	2
Gascoyne[5]	G1.24.63	15°31'S	110°00'E	10 Feb 63																	2
	G1.28.63	21°26'S	110°01'E	12 Feb 63				3											2		
	G1.29.63	23°10'S	110°00'E	12 Feb 63				2													
Gill[6]	2-74	34°24'N	75°36'W	10 May 53				2													
	8-9	28°20'N	79°48'W	12 Sep 54				3													
Lusiad II	H 1	01°16'N	103°52'E	28 Jun 62							6										
	H 7	06°58'N	79°50'E	28 Aug 62							3										
	29	05°02'N	53°01'E	31 Jul 62										1							
	45	05°00'S	62°00'E	14 Aug 62							1	4									
	51	00°57'S	62°19'E	17 Aug 62										1							
Lusiad V	46	00°02'N	58°52'E	30 Mar 63					4												
	48	00°01'S	63°00'E	1 Apr 63																	2
	50	00°00'	67°02'E	2 Apr 63					4												
	54	00°08'N	74°59'E	4 Apr 63				2	2					1							
	64	04°54'N	92°02'E	19 Apr 63										1							
	94	02°01'N	53°02'E	5 May 63										1							
Lusiad VII	75 H 7	00°28'S	10°51'W	4 Jul 63							6										
	MWT 14	32°29'S	09°04'E	6 Jun 63		1												4			
	MWT 19	31°11'S	00°56'E	9 Jun 63												2		5			
	MWT 79	00°55'N	11°29'W	6 Jul 63																1	
	Freetown	08°30'N	13°17'W	11 Jul 63						3											
Monsoon	7	09°11'S	127°33'E	22 Oct 60				2			2				2						
	9	13°19'S	109°35'E	7 Nov 60											2						
	11	11°15'S	103°32'E	20 Nov 60											2	1					
	13	17°01'S	93°29'E	25 Nov 60						1											
	22	37°50'S	85°22'E	26 Dec 60	2										2			1			
	24	39°18'S	119°51'E	9 Jan 61	2										2			1			
	26	64°11'S	165°56'W	13 Feb 61																	1
	31	32°35'S	160°56'W	8 Mar 61											2						
Naga	61-13	08°18'N	104°42'E	13 Jan 61								4									
	61-124	10°12'N	103°50'E	10 Feb 61								2									
	S10 61-107	09°19'N	103°58'E	10 Feb 61						4		4									
	S11A 61-198	09°11'S	115°33'E	27 Mar 61				2				11								2	2
	S11B 61-268	03°20'S	127°21'E	26 Apr 61																2	1
NORPAC	1 H	45°58'N	134°22'W	30 Aug 55												2	2				
	24-42H	40°26'N	146°37'W	21 Aug 55											1			6			
Scan	IV-1	33°49'N	139°10'E	15 Jun 69					5												
Shellback	90	06°01'S	95°46'W	26 Jun 52											2						
	109	03°41'S	81°30'W	4 Jul 52									1								
T. Washington	13	11°16'N	64°10'W	2 Jan 66							6										
TO-58-1 (Scot)	35	09°45'N	96°04'W	7 May 58																	4
Transpac	10 B	38°22'N	141°23'W	31 Jul 53											3						
	32 B	52°29'N	176°09'W	15 Aug 53												3					
	64 B	46°54'N	153°55'E	15 Sep 53												1					
Troll	40	31°10'N	128°48'E	10 Apr 55	3						2										
	45 A	31°17'N	137°29'E	12 Apr 55													7			1	1
	56	34°21'N	138°29'E	13 Apr 55					3												
Zetes	14	39°00'N	154°58'W	17 Jan 66														2			

* Species code:

A	*crassus*	G	*dentatus*	M	*californicus*
B	*longipceps*	H	*subcrassus*	N	*parki*
C	*monachus*	I	*inermis*	O	*langae*
D	*mucronatus*	J	*elongatus*	P	*sewelli*
E	*subtenuis*	K	*hyalinus*	Q	*attenuatus*
F	*pileatus*	L	*bungii*		

Unless identified by footnotes the samples are from the Marine Invertebrate Collections of Scripps Institution of Oceanography.

1 University of Rhode Island.
2 National Marine Fisheries Service, Galveston Laboratory.
3 Woods Hole Oceanographic Institution.
4 Bureau of Sea Fisheries, Cape Town, Republic of South Africa.
5 Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
6 National Marine Fisheries Service, Beaufort Laboratory.

remaining to be analyzed will not affect basic conclusions to be drawn about the sensilla and pores in *Eucalanus*. For purposes of this paper nomenclatural recommendations have been limited to an essential minimum. The species I recognize are summarized in Table 1. Aside from the integumental organs and dorsal and lateral views of the body, description of other characters is restricted to a few basic features (Figure 1).

Functional significance aside, the diagnostic qualities of body patterns of pores and sensilla should be examined in the Copepoda on a broad front.

MATERIALS AND METHODS

Systematic analysis of sensilla and pores was carried out routinely on adult females of all *Eucalanus* populations known to me (Table 1). Numbers of specimens and collecting localities are shown in Table 2. Sample size varied for each species according to its geographical distribution, the overall frequency of variation, number and arrangement of sensilla and pores, and the availability of specimens. The number of regularly occurring pores and sensilla on the body of a specimen is large, ranging from 80 to 140 depending on the species, and their unvarying arrangement in strongly patterned, bilaterally symmetrical arrays eliminated the need for examining large numbers of specimens in all but one case. Specimens were selected at random from within each zooplankton sample, but collecting localities were deliberately chosen to represent the known distribution of the species; i.e., as material on hand permitted representative specimens of each species were selected for examination from peripheral, intermediate, and central localities. Observations on adult males and on copepodite stages IV and V were also made on all species but were ordinarily limited to only two to four specimens each.

Sensilla and pores are exceedingly difficult to observe in *Eucalanus* using conventional light microscopy without staining and clearing specimens. Two simple methods were employed in this study. One served in examining general external features of the various types of sensilla and their proximity to glandular pores. Specimens were immersed for about 24 h in a combined clearing agent and stain, consisting of 9 parts lactic acid and 1 part of a 1% solution of chlorazol black E (CBE) in 70% ethanol. Specimens were then transferred directly to a drop of glycerol on a glass slide for microscopic examination.

More intensive clearing is necessary for accurate and systematic tabulation of body pores and sensilla. All tissue was removed from within the integument by heating specimens in a 10% aqueous KOH solution at 80° to 100°C for 2 to 4 h. Rapid boiling should be avoided to prevent the integument from breaking apart. The ratio of KOH solution to specimens was about 50 cc per individual. The KOH digestion was repeated using fresh solution if precipitates or fatty substances remained within the integument. The concentration of KOH has been increased on occasion to 25% with satisfactory results. For ease in viewing during microscopic analysis, it is essential in preparing the specimen to digest all tissues and eliminate precipitates from within the integument.

Following digestion the empty, still intact, exoskeleton is prepared for staining by a rinse in distilled water for 1 to 2 min and transfer to 70% ethanol for 1 to 2 min. These rinses should be repeated if flocculent precipitates remain within the integument. Immersion for about 30 sec in a solution of 1% CBE dissolved in 70% ethanol stains specimens intensely. Staining is terminated by flooding the preparation with distilled water and transfer of the specimen through a brief rinse in water to a drop of glycerol placed on a glass microscope slide for examination. Stained specimens suspended in glycerol may be stored indefinitely in appropriate slide storage boxes.

Washing and staining were carried out under a stereomicroscope using 3-spot deep depression slides and with solutions changed with the aid of finely drawnout glass pipettes equipped with rubber bulbs. Sensilla are usually lost in this process, leaving the stained cuticle punctured by clear perforations. Glandular pores also appear as clear perforations permitting light to stream through, but differ in shape and appearance of the margin as described below (p. 973).

Length measurements were carried out with the aid of a stereomicroscope at $24\times$ and $40\times$ magnifications depending on the size of the species. The microscope was equipped with a mechanical stage and an eyepiece reticle bearing a ruled scale of 100 divisions. Total length (TL) was taken from the right lateral view in two steps: one measurement along an imaginary line extending from the anteriormost tip of the forehead to the dorsalmost juncture between prosome and urosome (Fleminger, 1967) and the second along an imaginary straight line from the dorsalmost juncture of prosome and urosome to the posteriormost point on the right furcal ramus omitting the setae.

Examination of specimens for perforation number and distribution was carried out with the aid of a compound microscope equipped with a mechanical stage at magnifications of $150\times$ to $600\times$. A camera lucida was used in the preparation of drawings to approximate spatial arrangement of perforations in each form.

The outline drawing with perforations was reproduced by electrostatic duplicating machine for use on subsequent specimens of the species as a data recording form. Allowance was made for small variations in the distance between regularly occupied perforation sites; all missing and additional perforations were recorded on the form together with length measurements, sample, and specimen number. No attempt was made to estimate variability in the distance between adjacent perforations.

GENERAL OBSERVATIONS

Three general types of sensilla were found in *Eucalanus* (Figures 2, 3). They resemble relatively simple types found in other arthropods (e.g., see Snodgrass, 1935; Bullock and Horridge, 1965; Schneider, 1969) and are as follows:

1. Hair (trichodea) sensilla (Figure 2d); slender, elongated, uniformly attenuated, and unarmed; roughly 20 to 150μ in length and 1 to 5μ in diameter at the base; observed only on thoracic segments II to V.
2. Peg (basiconica) sensilla (Figure 2g); with pointed or rounded apex, ranging from 14 to 27μ in length, 1 to 3μ in diameter; they are widely distributed over the prosome and usually occur adjacent to the pore of an integumental gland.
3. Pit (coeloconica) sensilla (Figure 2i): shallow circular depressions in the integument, 3 to 6μ in diameter, the center raised in a nipple-like protuberance that stains intensively in CBE-lactic acid; they were observed in few species and only on the cephalon and anterior thoracic segments.

As a rule the sensilla are lost during the course of tissue digestion and staining. Perforations representing the sites of sensilla in prepared specimens appear under the light microscope as simple round openings. The innermost margin stains noticeably lighter than the surrounding integument. Large perforations ($\geq 4\mu$) from large hair sensilla may have a craterlike margin on the outer surface (Figure 2e). Under the light microscope the walls of the perforation may slope to form a larger elliptical outline on the inner surface of the integument. Perforations derived from pegs are simple and about 1 to 2μ across (Figure 2h). Perforations derived from pit sensilla appear as a pair of very small openings separated by a slender ridge (Figure 2j). One or more of the three types of sensilla were found on all segments of the cephalon and thorax. One aesthetask-like sensillum, usually weakly plumose, is present distoventrally on the furcal rami in all species. No other sensilla were observed on the urosome.

The other class of cuticular perforations are formed by the ducts of underlying integumental glands (Figure 2b). The glandular pore tends to vary from a semicircular to a slitlike opening of 4 to 7μ across the maximum dimension when viewed from above (Figure 2f-j). The margin stains as intensely as the surrounding cuticle and at least a section of the circumference turns inward toward the underlying hypodermis.

My use of the term pore in connection with integumental glands does not imply relationship to a different integumental feature, pore canals (Richards, 1951) discussed below.

Microscopic examination ($300\times$ to $600\times$ magnification) of intact specimens, especially those belonging to the elongatus group (treated

with CBE-lactic acid), frequently confirmed the connection between the pore and a single, gland-like, spherical to ovoid sac, roughly 30 to 75μ across the maximum dimension (Figure 2b), and not unlike the glands noted in other copepods (Fahrenbach, 1962; Clarke et al., 1962; Park, 1966). Integumental glands may occur on all the segments of the body (Figure 3).

A notable feature of the perforations (both sensilla and gland duct types) is their relationship to formation of the integument. Resembling that described in other arthropods (Dennell, 1960), the exoskeleton in *Eucalanus* has been observed in the present study to consist of prisms apparently laid down over individual cells of the hypodermis. The prisms are joined by interprismatic septa presumably of secreted procuticle that stains darker with CBE than the prisms. The organ-forming and neural cell extensions pass between cells of the hypodermis. Hence passage of these features through the integument occurs in the interprismatic septa, a feature frequently observed in this study in all of the species. In specimens with well differentiated prisms, numerous minute perforations formed by the pore canals (~0.1 to 0.3μ) may be seen within each prism. As Dennell (1960, p. 461) states, perforations observed on the surface of the cuticle formed by integumental organs and pore canals cannot be confused; the latter are numerous, minute, and within the margins of individual prisms; the former are an order of magnitude larger and lie in the septa between prisms. Pore canals were not considered in the analysis of *Eucalanus* perforations.

LIMITATIONS

Failure to obtain total elimination of tissue and precipitates in the hot alkali treatment and insufficient staining were the commonest sources of difficulties in carrying out microscopic examination of the perforations. Specimens that had moulted shortly before fixation and species in which the exoskeleton is relatively flabby (e.g., species of the elongatus group) require greater care in staining and handling.

Occasionally, areas of perforation size fail to take up as much stain as the surrounding

FIGURE 2.—Appearance of intact integumental organs and the perforations left by these organs in the integument of KOH-treated specimens of *Eucalanus subtenuis* (adult females). Specimens prepared for scanning electron microscope by Freon critical-point drying, vacuum coating with gold-palladium and examined with the aid of a Cambridge Stereoscan S.E.M. **a.** entire specimen in dorsal view; 1 mm $\cong$ 24.4 μ. **b.** schematic sectional view of typical combination of peg (basiconicum) sensillum and integumental gland with pore. **c.** thorax in dorsal view; 1 mm $\cong$ 8.5 μ. **d.** hair (trichodeum) sensillum; 1 mm = 1 μ. **e.** perforation in integument left by hair sensillum in KOH-treated specimen; 1 mm = 0.25 μ. **f.** pore of integumental gland; 1 mm = 0.25 μ. **g.** typical arrangement of peg sensillum (right) and pore (left). **h.** perforations in integument left by peg sensillum (right) and pore (left) in KOH-treated specimen. **i.** pit (coeloconicum) sensillum (left) and pore (right) of integumental gland. **j.** perforations in integument left by pit sensillum (left) and pore (right) in
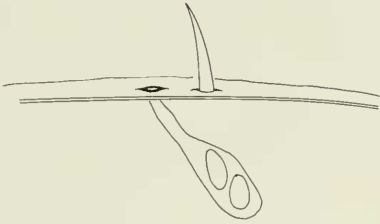
KOH-treated specimen. Figures g-j: scale, 1 mm = 0.5 μ.
(Reference to trade names does not imply endorsement
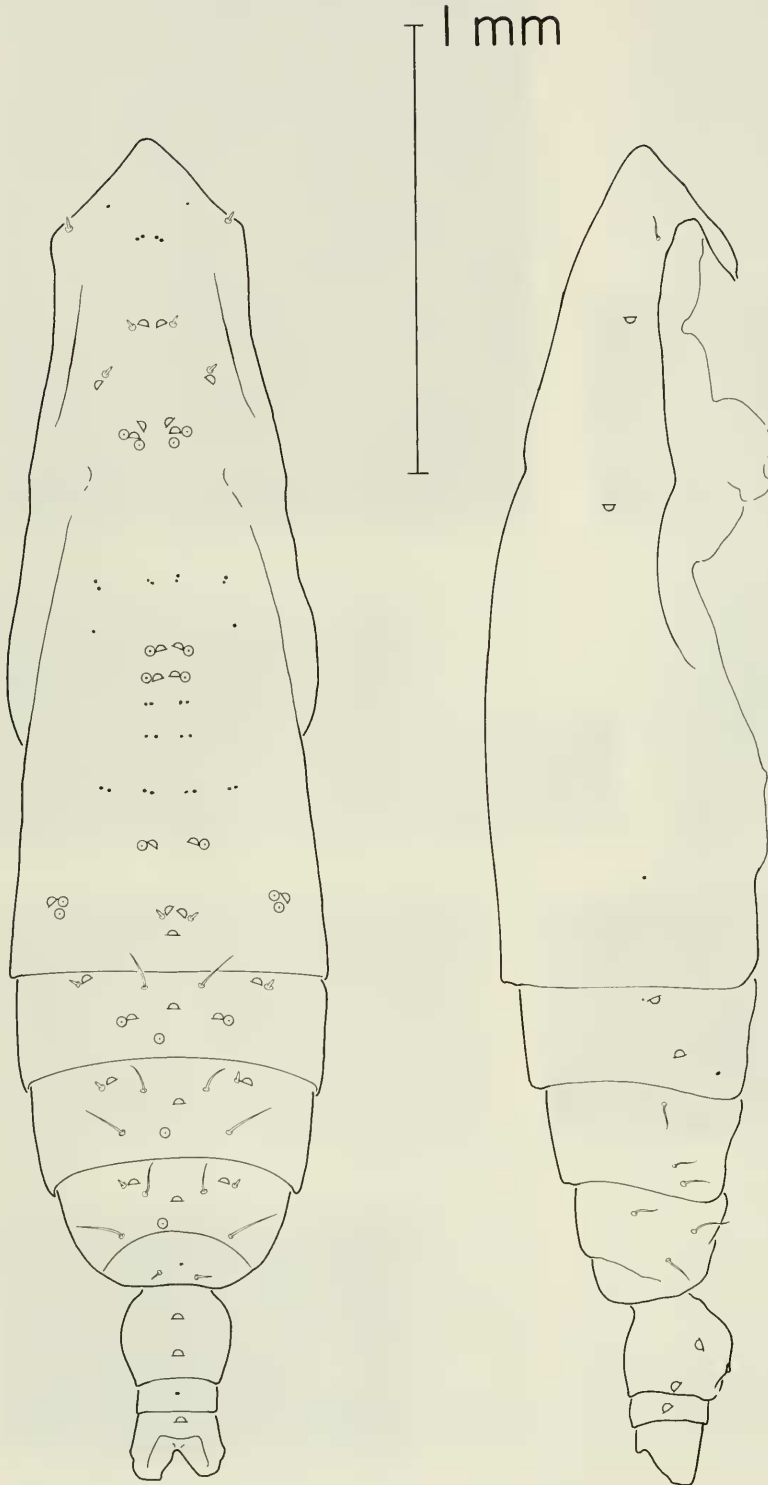by the National Marine Fisheries Service, NOAA.)

1 mm

FIGURE 3.—Distribution of sensilla and pores of integumental glands in an adult female specimen of *E. subtenuis*; dorsal view on left, lateral view on right. Hair sensilla are shown as curving, attenuated, and varying in length; peg sensilla are short, straight and blunt; pit sensilla are shown as an open circle with a dot in the middle. Pore of integumental glands shown as a half circle. Solid dots represent perforation sites observed in specimen after KOH-CBE treatment and represent organs missed during microscopic examination of the specimen before digestion of tissues; intact specimen cleared in CBE-lactic acid solution for 24 h prior to examination. All organs shown enlarged and schematically, though position is based on records obtained from camera lucida drawings; microscopic examination carried out at magnifications of from 150x to 600x.

integument and appear as light spots that may be mistaken for perforations. Direct comparison with a true perforation is helpful to note the reduced intensity of illumination passing through the light spot. Light spots tend to occur in the vicinity of usual perforation sites found in the genus and may represent incomplete or arrested development of a gland or sensillum. Light spots were not recorded as perforations.

A number of perforations relatively difficult to observe were not examined systematically. They include the dorsal surface of the furcal rami and cephalolateral sites in the vicinity of the first and second maxillae and the maxilliped. The ventral surfaces of the prosome appear to have few perforations but were not examined systematically.

DISTRIBUTION OF INTEGUMENTAL ORGANS

In each species the three types of sensilla and pores of integumental glands maintain essentially constant topographic relationships in arrangement and number on both the dorsal and lateral surfaces of the body, as seen for instance in *subtenuis* (Figure 3). One notable pattern appearing in all of the species for example is the distribution of dorsal hair sensilla, two appearing on the second thoracic segment, four on the third, and four on the fourth, the hairs always being arranged in transverse symmetrical rows, two hairs in each row (Figure 3). Another type of persistent pattern is the regular occurrence of the peg sensillum adjacent to the pore of an integumental gland (Figure 2). The organs are distributed in bilaterally symmetrical patterns that exhibit serial homologies. Serial homology is indicated by the partial to complete repetition of patterns in adjacent segments. As is shown below in the account of the different species, the closer the general morphological similarities between individual pairs of species the more similar the overall perforation patterns.

Every morphological type of sensillum or gland pore occupies a topographically unique position, i.e., a designated site within the framework of the overall bilaterally symmetrical pattern. The designated sites appear in KOH-treated specimens as morphologically distinctive perforations in the integument. Each body segment has a constant number of organs (Table 3) arranged in a distinctive pattern that is repeated with negligible variation within the series of specimens representing the species. Hence on an empirical basis the appearance of the same type of perforation in approximately the same topographic relationship in the series of specimens representing the species is compelling evidence that similarly positioned organs of the same type are homologous among individuals of the same species. That is, they appear to bear the morphogenetic relationships that are a primary basis for regarding the same cephalic or thoracic appendage among individuals of a population as being homologous. Thus the array of regularly appearing integumental organs (designated sites) among the individuals of the species is assumed to comprise a homologous set characteristic of the species.

Among the species of a species group, integumental organs appearing in topographically similar positions on the same body segment in all of the species are viewed as comprising a homologous set characteristic of the species group. The integumental organs common to the various species groups comprise the homologous set characterizing the genus. The implication of phylogenetic redundancies is seen in comparing perforation patterns among the species (see Figures 9, 11, 13, 15) presented below and in a segment-by-segment comparison of the number of regularly appearing sites in the species and species groups (see Table 3 and Figures 8, 9, 11, 13, 15).

In the case of a fused series of somites, i.e., a tagma such as the cephalosome, the patterns are arranged in accord with the sets of body appendages in the tagma. The number of homologous sites within the members of a species group is relatively high (cf. Figure 8 with Figures 9, 11, 13, 15) and the number of homologous sites within the genus (55) is remarkably high (Figure 6) considering that the species range from a low of 83 sites in *longiceps* to a high of 131 shared by *bungii* and *californicus* (Table 3).

TABLE 3.—Total number of lateral and dorsal perforation sites, by body and abdominal segments in ≥80% of *Eucalanus* specimens examined. Body segments indicated by corresponding appendages.

Genus & species	A1	A2	Mnd	Mx_1*	Mx_2*	Mxp*	P1	Total	P2	P3	P4	P5	Total	Abd 1+2	Abd 3	Abd 4	Abd 5	Total	Grand total
Eucalanus:																			
Number of homologous sites in genus	8	6	4	4	2	4	1	29	5	6	6	2	19	2	2	— ⏝ 1		5	53
subtenuis group:																			
subtenuis	12	6	10	10	4	4	17	63	14	18	15	3	51	6	2	1		9	122
mucronatus	8	6	6	6	4	4	9	43	12	14	13	3	42	6	2	1		9	94
crassus	8	6	8	6	—	4	5	37	11	13	13	3	40	4	2	1		7	84
longiceps	8	6	6	6	—	4	5	35	11	13	13	3	40	5	2	1		8	83
monachus	8	6	6	6	—	4	5	35	13	15	13	3	44	5	2	3		10	89
Number of homologous sites in group	8	6	6	6	—	4	5	35	11	13	13	3	40	4	2	1		7	82
pileatus group:																			
pileatus	8	6	6	8	—	4	5	37	11	14	14	3	42	5	2	3		10	89
subcrassus	8	6	6	10	4	4	9	47	15	18	14	3	50	7	4	1		12	109
dentatus	8	6	6	8	4	4	9	45	15	18	14	3	50	7	4	3		14	109
Number of homologous sites in group	8	6	6	8	—	4	5	37	11	14	14	3	42	5	2	1		8	87
elongatus group:																			
elongatus	10	6	4	6	2	8	7	43	7	10	10	4	31	8	4	4	1	17	91
hyalinus	12	6	8	6	10	16	9	67	9	11	10	4	34	7	4	4	1	16	117
inermis	14	6	8	4	6	12	11	61	7	10	9	3	29	4	2	—	3	9	99
bungii	12	6	6	4	12	16	15	71	13	14	12	4	43	8	4	4	1	17	131
californicus	12	6	6	4	12	16	15	71	13	14	12	4	43	8	4	4	1	17	131
Number of homologous sites in group	10	6	4	4	2	8	7	41	5	7	9	3	24	4	2	— ⏝ 1		7	72
attenuatus group:																			
attenuatus	12	6	4	6	4	12	11	55	13	16	16	6	51	8	2	7		17	123
sewelli sp.n.	12	6	4	6	4	12	11	55	13	12	12	6	43	6	2	5		13	111
parki sp.n.	12	6	4	6	4	12	11	55	13	12	12	4	41	7	3	5		15	111
langae sp.n.	12	6	4	6	4	12	11	55	13	12	12	4	41	8	3	10		21	117
Number of homologous sites in group	12	6	4	6	4	12	11	55	13	12	12	4	41	6	2	3		11	107

*Lateral perforation not counted.

VARIATION AT DESIGNATED SITES

As described above designated sites are those topographic positions on each segment occupied by an integumental organ of a morphologically specified type that occur within the context of a relatively fixed pattern on each segment. The pattern on each segment is primarily characteristic of the species and includes elements characteristic of the species group and of the genus as well.

No variation was observed in the morphological nature of the organ occupying the designated site during occasional examination of randomly selected intact specimens or in the characteristic type of perforation observed at the site in the sample of the species that was examined. Small differences in the relative distance between adjacent sites within the pattern of a segment were observed frequently. They are negligible, however, with respect to influencing the accuracy of recording details for each specimen. Replicate counts of the same specimens taken on subsequent days usually yielded similar results; the few departures from zero variation ranged from 1 to 3%. Spatial variation was not examined closely. Better understanding of its significance should be developed, as it probably reflects individual morphogenetic and possibly genetic differences.

Quantitative variation in terms of failure to find a perforation at a designated site or finding a perforation in excess of the regular number characterizing the segment (Table 3) is remarkably low. To the extent that spatial variability does occur, it may be argued that the basic

scoring of individual perforations as representing particular sites contains an element of judgment on the part of the observer.

Constant repetition of pattern (per body segment per species) in the distribution of perforations (see Figures 9, 11, 13, 15) and the small amount of variation in the total number of perforations observed in each species (Table 4) indicate that personal judgment by an experienced observer introduces negligible bias. The range about the mean number of perforations per species (Table 4) does not exceed 10% with exception of *subtenuis*, a special case actually representing three allopatric populations occupying separate regions of the world's tropical belt. Indeed, perusal of Table 4 indicates that quantitative variation is not a simple function of either sample size or total number of perforations.

With respect to presenting variation scored for each species, the frequency of a perforation appearing at each designated site is presented symbolically in three categories: sites occupied in all specimens, sites represented in 80 to 99% of the specimens, and sites represented in 10 to 79% of the specimens (see Figures 9, 11, 13, 15).

TABLE 4.—Number of localities, size of pooled sample, and number of observed perforations in species of *Eucalanus*.

Species	Localities	Specimens	Perforations		
			Range	$\bar{x}$	s
subtenuis group:					
subtenuis					
Atlantic Ocean	15	50	125-141	134.8	3.2598
Indian Ocean	10	24	119-139	130.0	4.9111
Pacific Ocean	10	36	114-135	123.6	4.9750
mucronatus	6	20	86-91	89.4	1.5355
crassus	4	11	83-85	84.0	0.4713
longiceps	4	12	79-83	82.7	1.1572
monachus	5	17	87-91	88.8	0.8106
pileatus group:					
pileatus	8	21	85-94	90.5	2.0384
subcrassus	9	34	109-117	110.1	2.4722
dentatus	5	24	109-115	111.5	1.3313
elongatus group:					
elongatus	11	19	90-101	94.9	3.3154
hyalinus	14	25	109-121	114.8	3.2490
inermis	7	16	94-106	99.7	2.7500
bungii	5	15	127-133	130.1	1.8086
californicus	6	23	125-135	131.2	2.1829
attenuatus group:					
attenuatus	16	26	117-126	122.0	2.0703
sewelli sp.n	24	43	107-113	110.3	1.2070
parki sp.n.	5	18	109-114	111.5	1.3323
langae sp.n.	7	14	115-121	117.6	1.7388
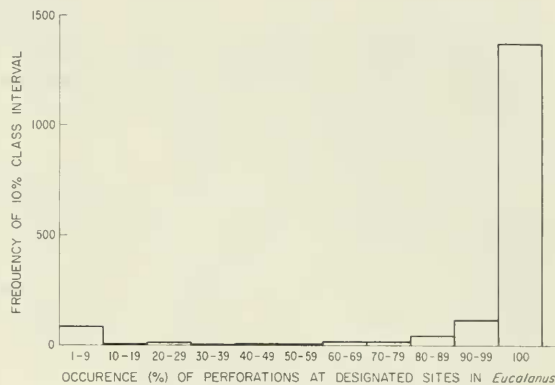
FIGURE 4.—Frequency of occurrence of perforations at designated sites on the dorsal and right lateral integument of *Eucalanus*. The frequencies found in each species are grouped in class intervals of 10% and each class is summed for all species. Each designated site represents the occurrence of a particular type of integumental organ appearing in a KOH-treated specimen as a distinctive perforation in the integument and occupying a topographically unique place within the framework of the overall bilaterally symmetrical pattern found in the species. For purposes of this graph the appearance of such a distinctively placed perforation in only one specimen of the pooled sample for the species is sufficient to include it among the number of designated sites found in the species. Graph based on examination of 448 adult female specimens representing 17 species that yielded a total of 1,709 designated sites as defined above.

Sites found in less than 10% of the sample have been omitted. A general summary of the variability at each site is presented in Figure 4. Roughly 80% of the sites were represented by a perforation in every specimen. In 10% of the sites a perforation was observed in 80 to 99% of the sample. The remaining 10% of the sites were occupied at lower frequencies, but this category includes a number of sites that show remarkable patterns of geographical variation in *subtenuis* that are discussed below.

Designated sites do not vary with respect to type of organ they represent, but one class of variation in topographic relationship is noteworthy. As mentioned above, peg sensilla regularly occur adjacent to the pore of an integumental gland. The peg and pore pairing often varied with respect to the position of the two relative to the orientation of the segment. The peg tends to be lateral to the pore, but this may be completely reversed or appear at any intermediate stage about a 360° arc. As a pair, how-

979

ever, they occupy a discrete position relative to the remainder of the sites on the segment. This class of variation also deserves increased attention as a potential fine scale indicator of intrapopulation genetic variation.

Thus for application of integumental organs to copepod systematics at or above the rank of species, variation encountered during this study appears to be of no consequence. Moreover, the intraspecific variability observed may on the basis of experience with *subtenuis* provide a dependable, measurable source for studying population homogeneity and gene flow.

PERFORATION SITES IN THE GENUS

Intra- and interspecific comparisons of perforation number and arrangement are facilitated by compelling evidence that sites similar in location and associated organ (i.e., gland pore or sensilla type) within and between species are homologous. Tables 3 and 4 and figures of individual species summarize the evidence that in general perforation number and topographic arrangement are essentially constant and characteristic for each species. Further, all of the available observations indicate that the type of organ found at any particular perforation site is also constant.

As shown below, constant differences in numbers and arrangement of perforations between the morphologically more similar species are small. Quantitative and topographic differences are correspondingly greater between species that are more dissimilar morphologically (e.g., Figures 9, 11, 13, 15). However, the total number of perforation sites in the genus appears to be about two times the number found in any one species (Figure 5).

To construct Figure 5 an assessment of the extent of interspecific homology in sensilla and pores of *Eucalanus* was obtained by rigorous comparison of all the species segment by segment. The tabulation was restricted to designated sites, i.e., those occurring in 10% or more of the specimens of each species. As described above, sites are judged to be homologous if they occur on the same segment in the same general position relative to the pattern characteristic

of the segment and represent the same kind of organ (gland pore or type of sensilla). The place of insertion of the segment's paired appendages and the topographic position relative to the other sensilla and gland pores of the segment aid in locating perforation sites. Overlaps of camera lucida sketches were also helpful when allowance was made for relative and absolute differences in size. Allowance was also made for small-scale variation of one or two perforations relative to another one or a set as in peg and pore pairings; small differences in the spacing between adjacent sites and rotation of one site relative to another was observed frequently within the general pattern arrangement of individual species.

The analysis reveals 163 different dorsal pore and sensilla sites and 30 lateral sites on each side of the body. The total number of different sites within the genus (223) is less than twice that of the species with the highest individual score (Table 3). Thus most sites in the genus appear to be common to many of the species and an appreciable number is common to all (Figure 6).

Examination of small numbers of copepodid stages IV and V, adult males of all species and a few specimens of copepodid stage III indicated conformity of each to the pattern characteristic of the species, except for segments that undergo sexual modifications in the process of maturation.

PERFORATION NUMBERS AND PATTERNS AMONG THE SPECIES GROUPS

Interspecific comparison of the perforations observed in *Eucalanus* is, as already mentioned above, greatly simplified by the not unreasonable assumptions that repetitious similarities in pattern are dependent upon and a direct reflection of genetic similarities. With this as a working hypothesis, reducing and assimilating the distribution of perforation sites was enhanced by assembling similarities among the different species and by using for comparisons all other constant topographic features of the integument.

All the species have in common 37 tergal sites, best seen in dorsal view and 9 pleural sites
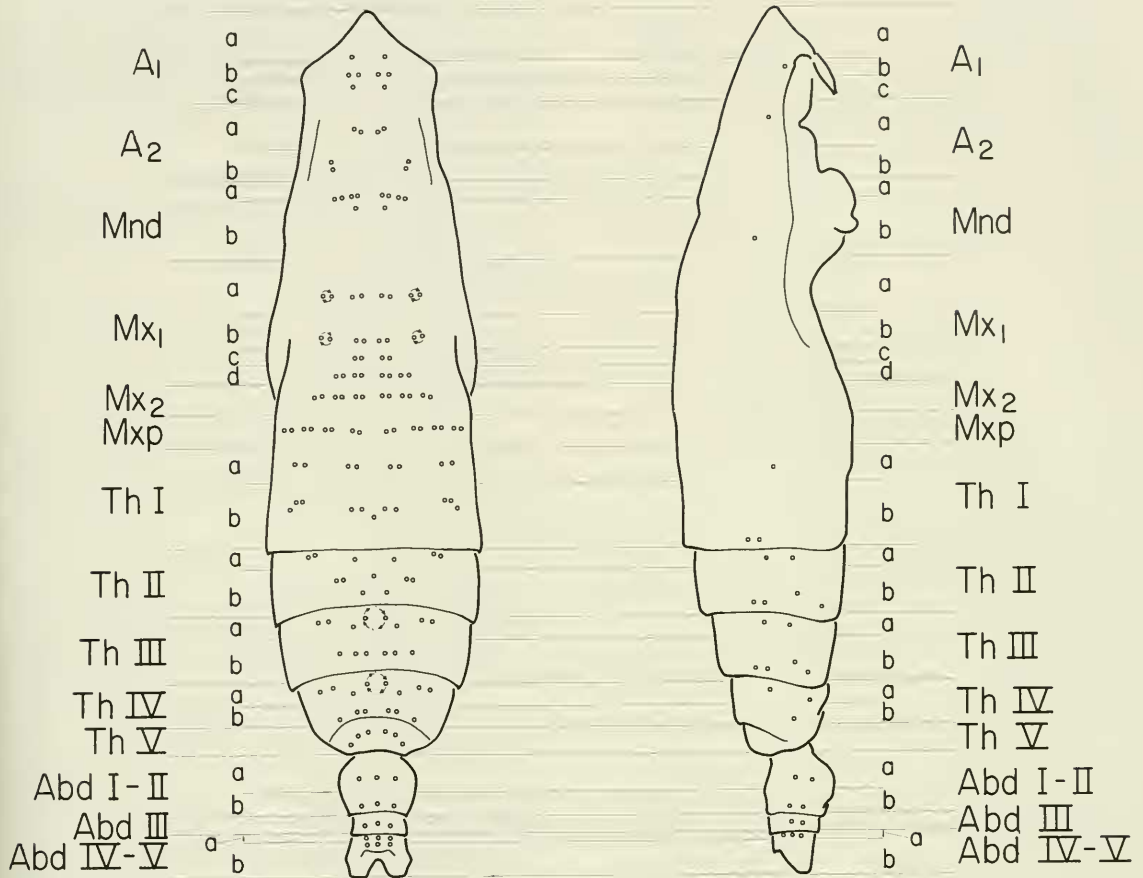
FIGURE 5.—Schematic presentation of all designated sites observed in adult female *Eucalanus*. Open-ended system for designating individual sites provided by abbreviations of appendages or abdominal segments together with row (a, b, ...) and in dorsal view number to left or right of midline, or in lateral view number in dorsal to ventral order.

Cephalosome in *Eucalanus* contains the cephalon extending from the first antennae (A1) to the second maxillae (Mx2), the maxillipedal somite (Mxp = Th0) and the first pedigerous somite (ThI). Thoracic segments ThII, ThIII, ThIV bearing swimming legs 2, 3, and 4 are separate from one another, but ThV lacking a pair of swimming legs in the female is partially fused to ThIV. In the female abdomen the first two somites are fused (Abd.I-II) during maturation of the genital segment. Abd.III is separate and Abd.IV is separate in the elongatus species group but fused to Abd.V in the other three species groups. The furcal rami are fused to Abd.V in all the species.

on each side, best seen in lateral view (Figure 6). Tergal sites on the cephalosome are pores and peg sensilla; on ThII to ThV, all but two (ThII-mb and Abd.IV-V-m) are hair sensilla; the two exceptions are pores. The pleural sites of the cephalosome appear to include both pores and peg sensilla. Pleural sites on ThII to ThIV are hair sensilla and those of the urosome are pores.

Within the genus four groupings may be distinguished by virtue of additional perforations that appear in common only among the species comprising each group (Figure 8). Additional support for these groupings may be found in other morphological characters of taxonomic value in *Eucalanus* such as segmentation of the abdomen and the shape of the seminal receptacles in females (Figure 1), fifth legs of adult males, and various details in the appearance of the cephalosome. The groupings and their complement of species and geographical forms are listed in Table 1.
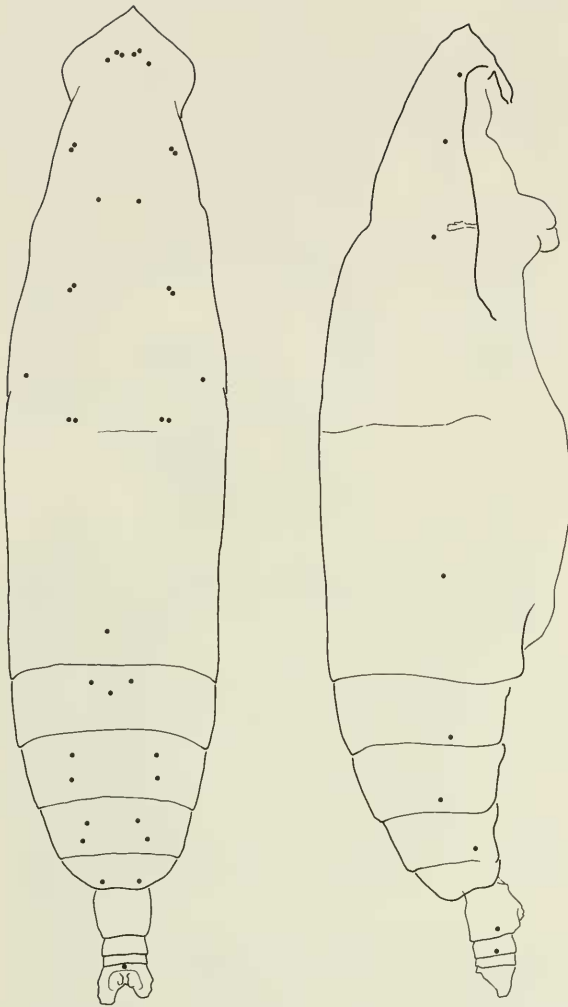
FIGURE 6.—Designated sites (represented by a dot) occurring at frequencies of ≥80% within the pattern of each species and present in every species of the genus *Eucalanus*. Dorsal view on left, lateral view on right; outline of organism based on *elongatus* used solely as vehicle to show topographic relationships of sites.

The Subtenuis Group

Sites distinguishing the subtenuis group (Figure 8c) appear on various portions of the cephalosome and thorax. On the cephalon the mandibular somite bears two pairs of tergal sites. ThI shows only three sites arranged in a transverse row. ThIII and ThIV are similar, both being characterized by bilateral tergal pairs lying outside and anterior to the quadran-gle of hair sensilla and a single medial site slightly posterior to the anterior hair sensilla. The subtenuis group contains five generally accepted species that occur typically in eutroph-ic oceanic waters.

Sites in *E. crassus* (Figure 9a) are identical with the pattern of the species group except that the perforations of row a on the mandibular somite are increased to two pairs (Mnd T-a-*l*1, *l*2 and r1, r2).

E. longiceps differs from the group pattern solely by the presence of a single mediodorsal site on the genital segment (Figure 9b).

E. monachus (Figure 9c) differs from *longi-ceps* in two features: the occurrence of a trans-verse row of three tergal sites across Abd.IV-V and three pleural sites on ThII, ThIII, and ThIV.

E. mucronatus (Figure 9d) shows a small increase in the number of sites. On the cepha-losome up to six pairs of tergal sites may appear in addition to the group number between the somite of the second maxilla and the maxilli-pedal somite. ThI shows an additional tergal pair on either side of the middorsal site. ThII and ThIII have an additional site in the posterior row (ThII T-b-*l*1 and ThIII T-b-*l*1) to the left, but the symmetrical homologue to the right of the middorsal axis is absent. On the abdomen the genital segment has two middorsal sites and Abd.III may have one.

E. subtenuis (Figure 9e) has the largest num-ber of regular perforation sites in the genus. Dorsally, in addition to the species group num-ber, two more pairs appear in the somite of the second antenna, up to eight more pairs between the somites of the first and second maxillae, four more pairs on the maxillipedal somite, four more pairs on ThI, and two more pairs on ThII. ThII and ThIII have a single asym-metrical tergal site (pore) within the quadrang-le formed by the hair sensilla as in *mucronatus*. Laterally, ThII and ThIII both show one or more pairs on either side.

Within the group, *subtenuis* shows the largest number of perforations (Figure 10) and the most extensive geographical distribution relative to areal extent and sympatry (unpublished). Differences between *subtenuis* and its closest cognate, *mucronatus*, are concentrated in the

ThIT-a-/4   -/1   -a-r1   -r4

ThIT-b-/5   -/1   -mb   -r1   -r5

ThII T-a-/3   -/1   -mb   -r1   -r3

ThII T-b-/2   -r2

ThIP-ra

ThIP-rb-1   -rb-2

ThII P-ra-1   -ra-2

ThII P-rb-1   -rb-4
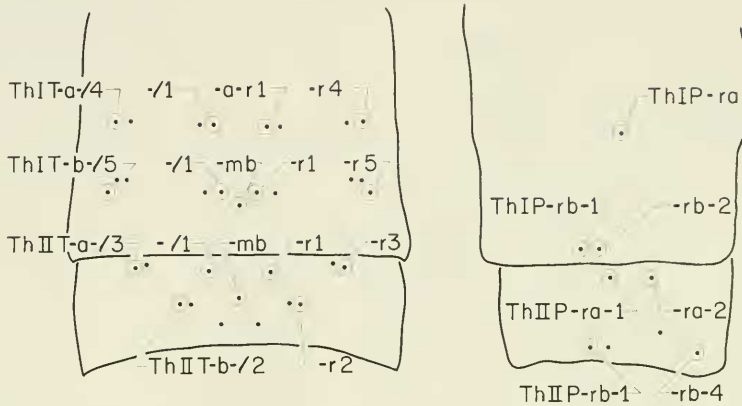
FIGURE 7.—Scheme for codifying designated sites in *Eucalanus*. Left: dorsal view of posterior portion of cephalosome and thoracic segment 2. Right: lateral view of same.

First unit of code for referring to a designated site is reference to the somite, using the appropriate appendage in the case of the cephalosome or the body segment (ThII, ThIII, . . ., Abd.I-II, Abd.III, . . .). Second unit indicates whether it is dorsal, i.e., tergal (T), or lateral, i.e., pleural (P). Tergal sets are grouped in transverse rows. Thus, perforations are designated as being on the right (r) or left (l) of the mid-sagittal plane and are numbered from the medialmost to the lateralmost (1, 2, . . .). Transverse rows are lettered in an anterior-to-posterior sequence (a, b, . . .). Perforations falling on the midsagittal plane are termed medial (m) and lettered in an anterior-to-posterior sequence (a, b, . . .).

Both right (r) and left (l) lateral, i.e., pleural (P), sets are numbered in a dorsal-to-ventral sequence (1, 2, . . .). For convenience anterior-to-posterior division into rows is utilized following the corresponding set of tergal sites and are also lettered in an anterior-to-posterior sequence.

Various sites in dorsal and lateral views in the figures are codified according to the scheme proposed above.

the tagma also showing the most extensive geographical variation. Geographical variation in *subtenuis* distinguishing the Indian, Atlantic, and East Pacific populations is discussed below (p. 999). The other four species fall within a narrow overlapping range (> 80 to < 95 perforations). Differences in number and arrangement especially in the genital segment characterize *crassus* and *mucronatus*, the two species overlapping geographically in the Indian and West Pacific Oceans. Differences in number and pattern also involving the genital segment distinguish *crassus* and *monachus* which co-occur in the Atlantic Ocean. *E. crassus* also differs from *longiceps*, a temperate species of the Southern Hemisphere, and from *subtenuis* in the sites on the genital segment.

The Pileatus Group

The pileatus group (Figure 8d) consists of three sibling species that are only weakly differentiated in general appearance from that of the subtenuis group. The pileatus group also strongly resembles the subtenuis group in perforation pattern, the primary differences being in a small increase in the number of middorsal sites on the thoracic segments. One additional pair occurs on the somite of the first maxilla, and single anterior middorsal sites are found on ThIII and ThIV. Three tergal sites may appear on the genital segment, but the posterior two of the three sites are irregular in occurrence in *pileatus;* therefore, at the species group level, the genital segment is best characterized by a single middorsal site.

Among the individual species *E. pileatus* is essentially undifferentiated from the pattern in the species group (Figure 11a). It lacks tergal sites on the somite of the second maxilla and on Abd. III, although it has three tergal sites across Abd.IV-V. It also lacks posterodorsal pleural sites on ThI, ThII, and ThIII. The genital segment may have one or two posterotergal sites in addition to the regular middorsal site.

E. dentatus and *subcrassus* share a number of features that separate them from *pileatus*, namely two tergal pairs of sites on the somite of the
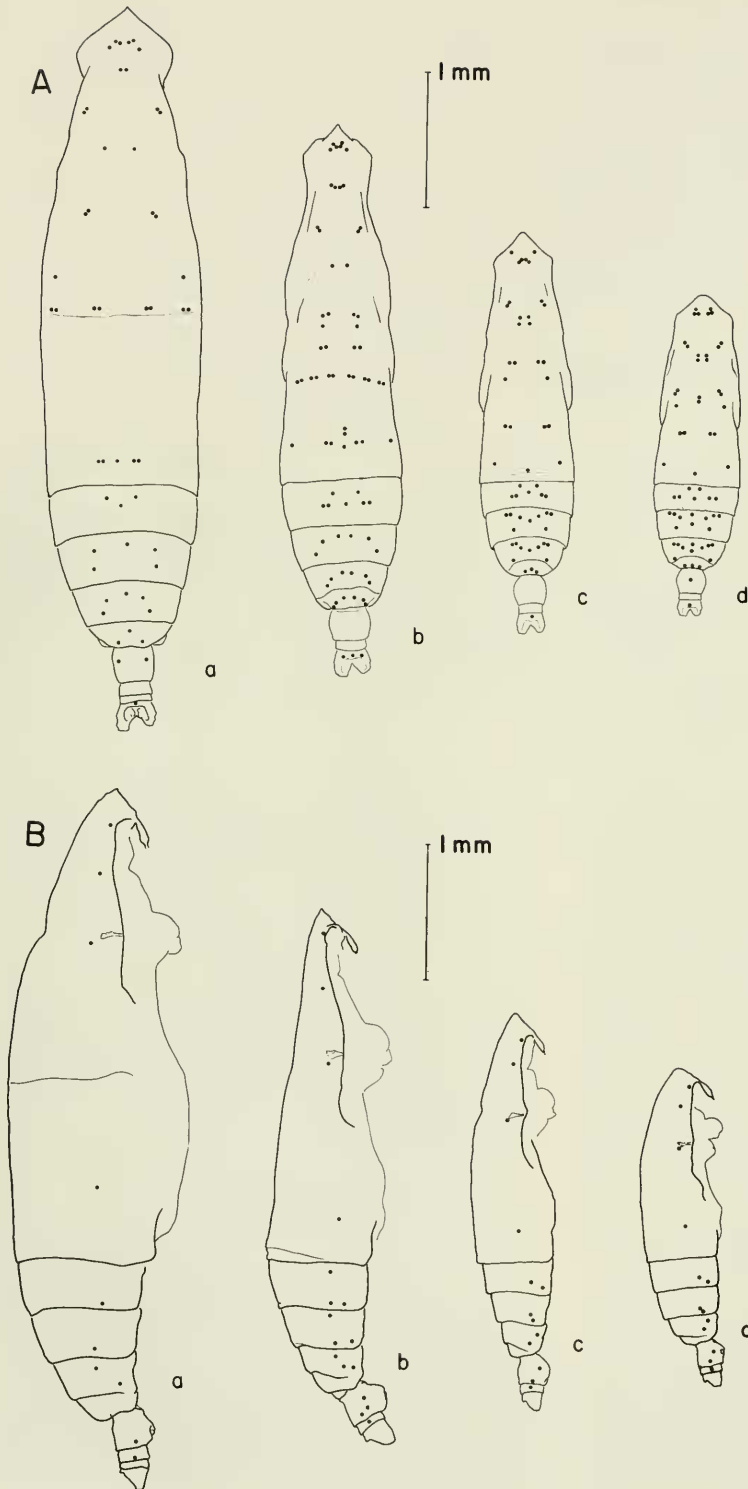
FIGURE 8.—Sites common to each species group of *Eucalanus*. From the left, **a.** elongatus group, **b.** attenuatus group, **c.** subtenuis group, **d.** pileatus group. A, dorsal view. B, right lateral view.
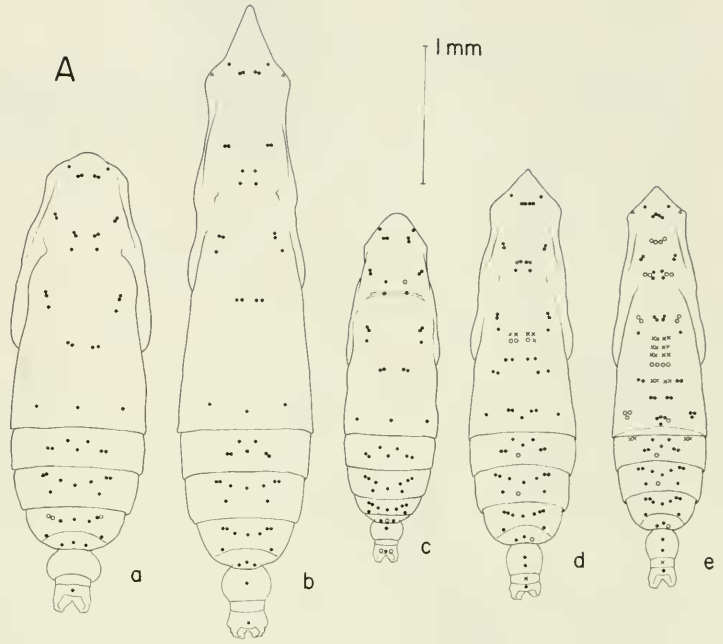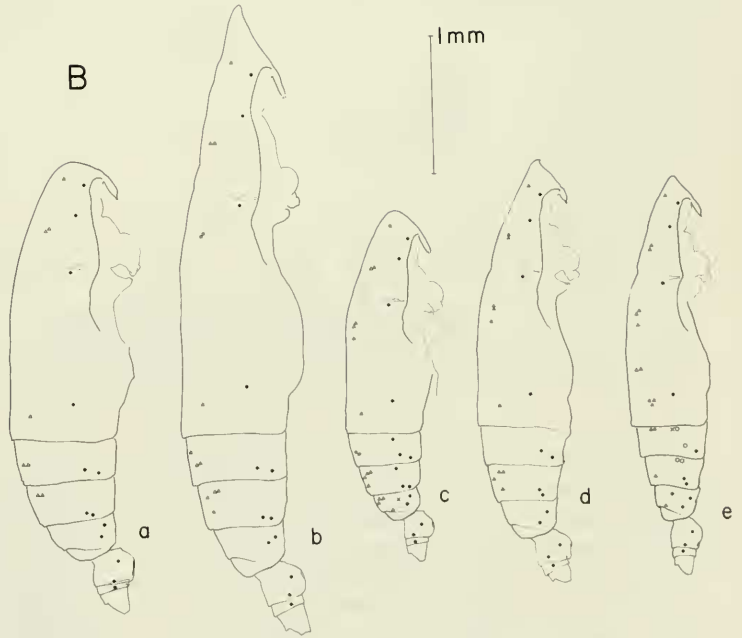
FIGURE 9.—Species of the subtenuis group of *Eucalanus*: **a.** *crassus*, **b.** *longiceps*, **c.** *monachus*, **d.** *mucronatus*, **e.** *subtenuis*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. A, dorsal view. B, lateral view. All figures of adult females made with the aid of a camera lucida.
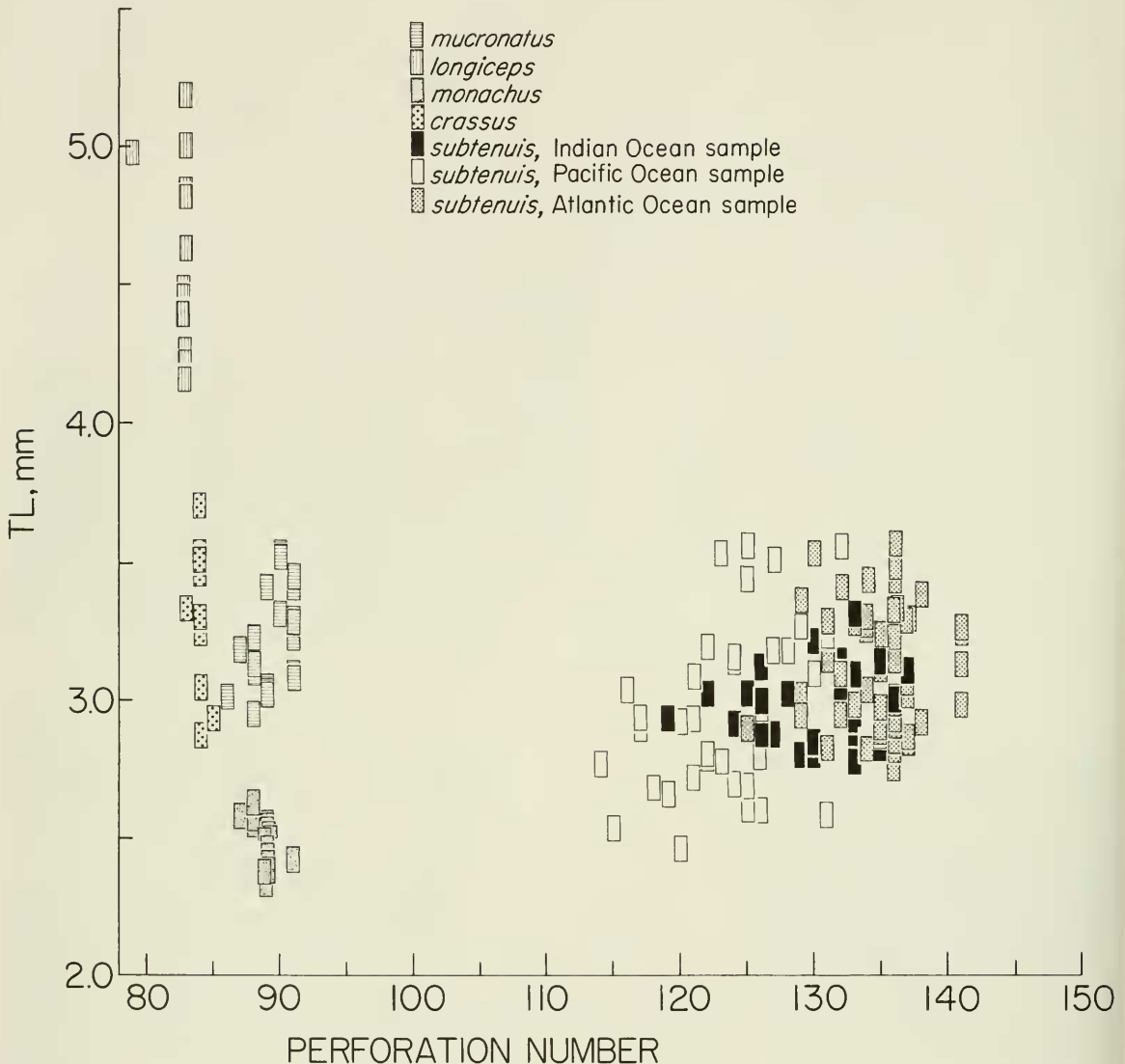
FIGURE 10.—The subtenuis group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

second maxilla, three tergal sites regularly on the genital segment, two or more tergal sites on Abd.III, and, laterally, a pair of posterodorsal pleural sites on each side of segments ThI, ThII, and ThIII. *E. dentatus* (Figure 11b) shows, in addition, three tergal sites across Abd.IV-V while *subcrassus* (Figure 11c) has a single mid-dorsal site on Abd.IV-V.

As in the subtenuis group the species with the most extensive geographical range, the circumglobal *pileatus*, shows the most distinctive number of perforations within the species group (Figure 12). Differences between *subcrassus*, a broadly neritic species of the Indian and Pacific Oceans, and *dentatus*, a coastal species of Austral-Asian seas, are limited to arrangement, the number of perforations shown by the pooled samples of the two species being equal.
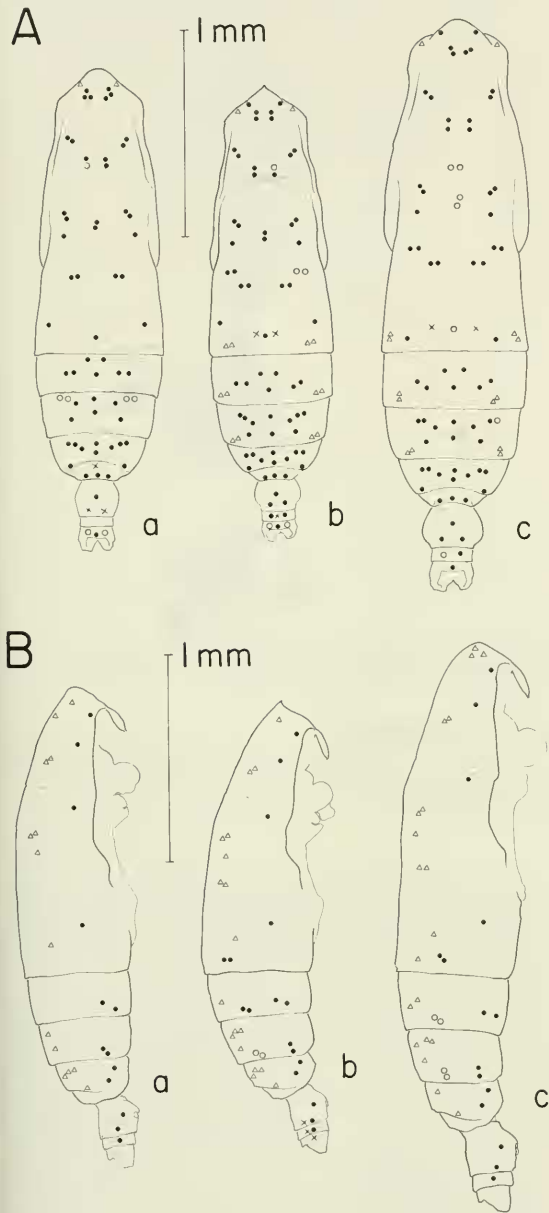
FIGURE 11.—Species of the pileatus group of *Eucalanus*: **a.** *pileatus*, **b.** *dentatus*, **c.** *subcrassus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view above, lateral view below. All figures of adult females made with the aid of a camera lucida.

The Elongatus Group

Species of the elongatus group are characterized by 1 pleural and 23 tergal sites in addition to the 37 and 9, respectively, present in the genus (Figure 8a). The increase represents the sum of one pair in the forehead (A2T-a-*l*1 and r1), two pairs on the maxillipedal somite (MxpT-*l*3, *l*4 and r3, r4), two pairs on the first free thoracic segment (ThIT-*l*1, *l*2 and r1, r2), one medial site each on ThIII, ThIV, and ThV, two dorsal sites on the genital segment, and one additional pleural site on each side of ThIV.

E. inermis (Figure 13a) is distinguished in dorsal view by the following tergal sites: a set of eight on the A1 somite, five on ThIV, three on ThV, two on the genital segment, none on Abd.-III and Abd.IV, and three on Abd.V. In lateral view diagnostic pleural sites on either side include one on the genital segment and none on Abd.IV.

E. elongatus (Figure 13b) differs from each of the other species in the group in a number of details but only the two anterior tergal sites on the second antennal somite (A2T-a-*l*1 and r1 and the tendency for more than two sites on Abd.III and Abd.IV are uniformly diagnostic within the group.

E. hyalinus (Figure 13c). Single tergal sites on ThI (ThIT-a-*l*1 and r1) and the three tergal sites on the genital segment distinguish *hyalinus* from the other species of the group.

E. californicus (Figure 13d). Sites that distinguish *californicus* from the preceding species are the pair middorsal on the somite of the second maxilla, the pair on the first free thoracic segment (ThIIT-a-*l*1, *l*2 and r1, r2), the pair flanking the median site on ThII (ThIIT-b-*l*1, *l*2 and r1, r2), and in lateral view the three pleural sites on either side of ThIV. No consistent difference in number or in arrangement of perforation sites was found that distinguishes *californicus* from *bungii*. Both species are morphologically distinctive in other respects (e.g., setation of the mandibular basis) and share a common boundary across the North Pacific, *californicus* occupying the temperate zone and *bungii* occurring to the north, without any apparent evidence of intergradation or hybridization.
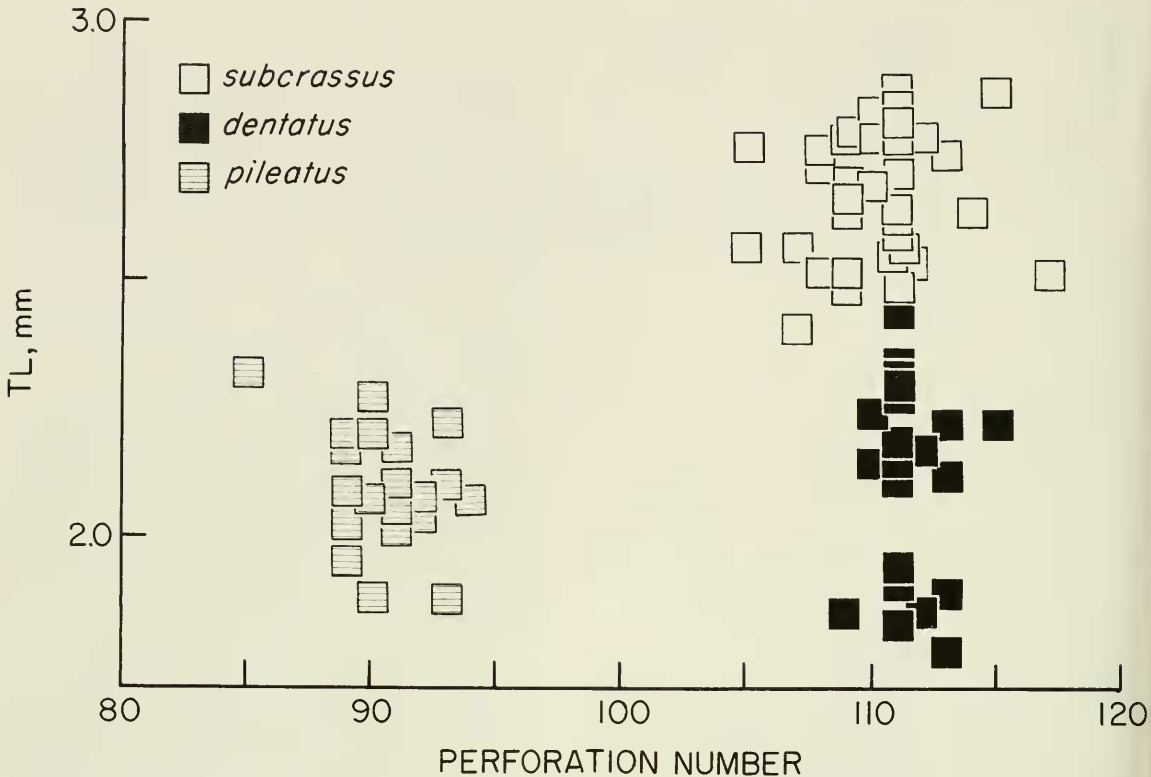
FIGURE 12.—The pileatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

As in the two preceding species groups a relationship between distinctiveness in overall number of perforations and geographical distribution is shown by the elongatus group (Figure 14). The only circumglobal species of the group, *hyalinus*, occupies a distinctive position with respect to perforation number. The two species to the left, *inermis* and *elongatus*, are geographically isolated from one another and the two species to the right, *bungii* and *californicus*, are biogeographically separated from one another. The distribution of *hyalinus* in contrast brings reproductively ripe individuals into contact with all of the other species except *bungii* (unpublished data).

The Attenuatus Group

Members of the attenuatus group have in common 38 tergal and 8 pleural sites added to the primary generic number (Figure 8b). The increase is widely dispersed about the body being found anteriorly on the second antennal somite (A2T-a-*l*1, *l*2 and r1, r2), the somite of the second maxilla (Mx2T-*l*1, *l*2 and r1, r2) and on the maxillipedal somite, where six pairs occur, two pairs more than in the elongatus group. Adding to the characterization are the anterior middorsal pair of ThI, the six symmetrically arranged tergal sites of ThV and the three tergal sites of Abd.IV-V. In lateral view pleural sites are also more numerous, three pleural sites on each side being found on ThII, ThIII, ThIV, and on the genital segment. Every segment except Abd.III bears more sites than the number characterizing the genus, and the group total of 109 sites is the largest among the four groups of species in *Eucalanus*.

Four discrete populations of *attenuatus* s.l. emerge from the present study. They are mor-
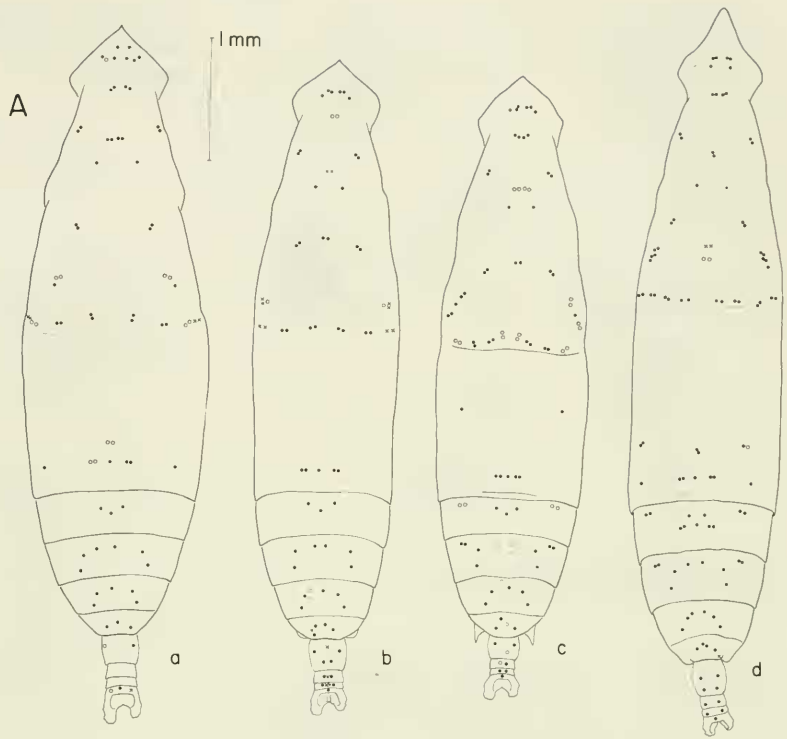
FIGURE 13.—Species of the elongatus group of *Eucalanus:* **a.** *inermis,* **b.** *elongatus,* **c.** *hyalinus,* **d.** *californicus.* Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view above, lateral view below. All figures of adult females made with the aid of a camera lucida.
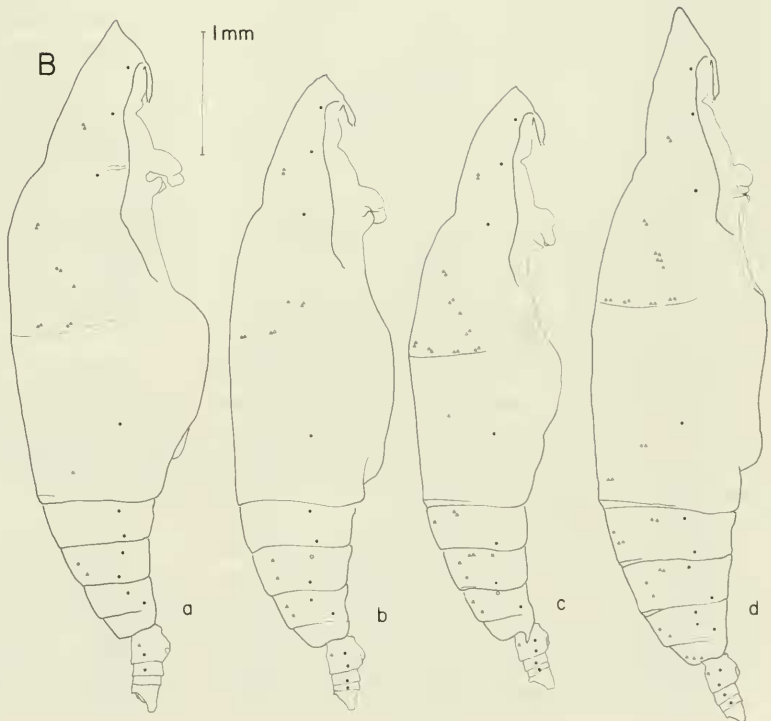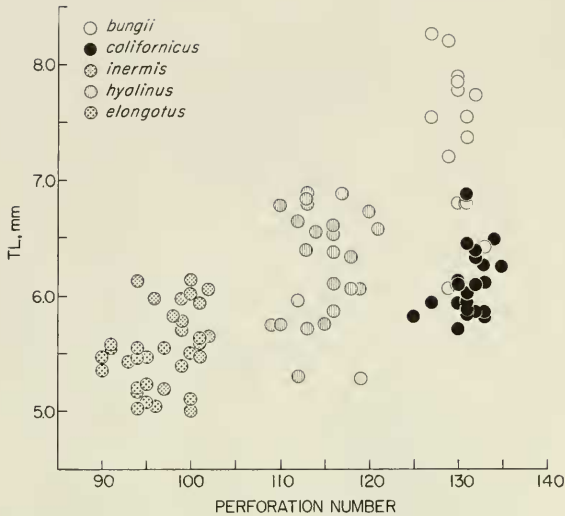
FIGURE 14.—The elongatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

phologically distinguished primarily by the number and arrangement of integumental organs and biogeographically by inferred distributions derived from the very different sets of geographical localities available for each form. In this regard it is important to stress that the sampling localities were chosen to represent the geographical extent of each population from hundreds of localities of *attenuatus* s.l. obtained during the course of global studies on several calanoid genera. In the case of the two unusually large species, *parki* and *langae*, the geographical records represent all that are on hand. A major factor favoring separation of this complex into four distinct species is the pattern seen in the preceding three species groups and repeated in the attenuatus group. That is, the species with the broadest geographical range also shows the most distinctive number or arrangement of sites, especially on the genital segment, and that related allopatric species may show little or no difference in these features.

In each instance the diagnosis is based on the adult female and stresses those designated sites characterizing the species within the group. Thus despite the more formal presentation and the addition of nonperforation data essential to describe each species the information on num-

ber and arrangement of designated sites is readily available within the diagnosis for each species.

Eucalanus attenuatus (Dana, 1849), *sensu stricto*
(Figures 1q, 15d, 18a, g, j, k, n, q)

E. attenuatus Dana, 1849, p. 18; 1853, p. 1080, Pl. 75, Figs. 2a-d; Vervoort, 1946, p. 95-103 (pars), Figs. 7a-c.
E. pseudattenuatus Sewell, 1947, p. 39, Test fig. 7A. NEW SYNONYMY.

Diagnosis: Adult female: Characterized by having the largest number of designated sites among the species of the attenuatus group (Figures 15d, 16; Tables 3, 4). Sites in addition to those of the species group include two pairs of tergal sites on ThIII (ThIIIT-b-*l*1, *l*2 and r1, r2), two similar tergal pairs on ThIV, two tergal sites on the genital segment, a single transverse row of three tergal sites on Abd.IV-V and, laterally, three pleural sites on either side of Abd.IV-V (Figure 15d). Length of triangular forehead extending beyond the lateral lobes overlying the first antennae usually shorter than width at origin, apex acute in lateral view and not curving ventrad (Figure 15d). Mandibular basis with two setae.

Adult male: Thoracic tergal sites as in female. Abd.II with two tergal sites (Figure 18j). Mandibular basis with two setae. Forehead weakly produced beyond base of rostrum, apex broadly rounded in dorsal and lateral views (Figure 18g, k).

Additional description: Female lacking fifth pair of legs, abdomen with three separate segments (Figure 15d). Male left fifth legs with four segments, right leg about half as long and trimerous (Figure 18q).

Total length: Adult female: range 3.63 to 4.65 mm, mean = 4.10 mm, $s = 0.2900$, $N = 28$ (Figure 16).
Adult male: range 2.93 to 3.50 mm, mean = 3.135 mm, $s = 0.1775$, $N = 7$. Specimens selected at random from localities listed in Table 1.
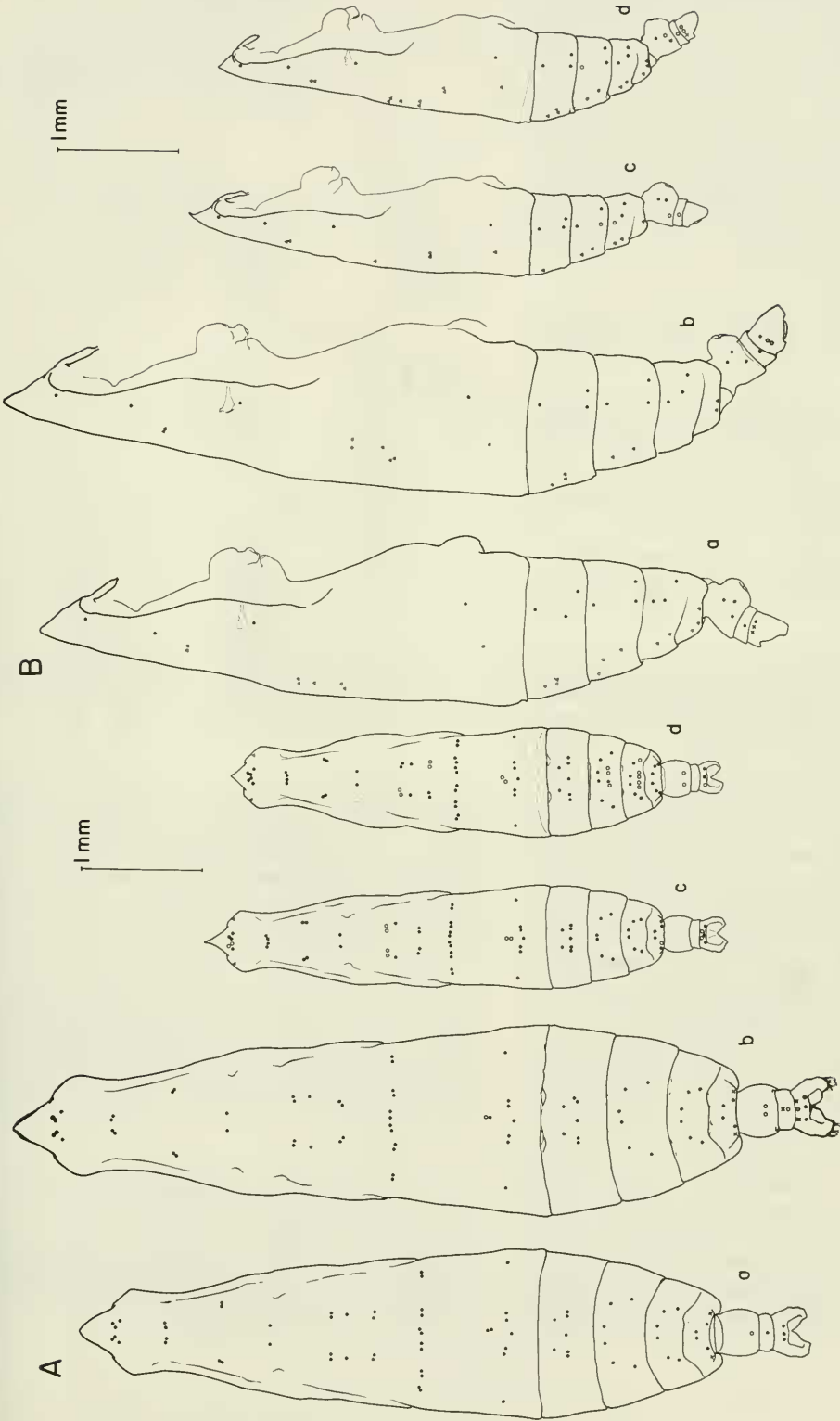
FIGURE 15.—Species of the attenuatus group of *Eucalanus*: **a.** *parki*, **b.** *langae*, **c.** *sewelli*, **d.** *attenuatus*. Dots represent sites occurring at a frequency of 100% in the pooled sample of the species; open circles are sites appearing in 80 to 99% of the pooled sample; crosses are sites occupied in from 10 to 79% of the pooled sample. Open triangles are sites also visible in lateral view but assigned to tergal sets. Dorsal view on left, lateral view on right. All figures of adult females made with the aid of a camera lucida.

Geographical distribution: Verified localities (Figure 17) suggests a broadly tropical distribution restricted to the Indian and Pacific Oceans. A deliberate search among several hundred plankton samples from Atlantic Ocean localities scattered over the lower latitudes failed to yield a single specimen of *attenuatus* s.s. The species is widespread in tropical latitudes of the Indo-Pacific but appears to be most abundant immediately downstream of eutrophic regions along the equator.

Reference: Three lots of reference specimens deposited in the U.S. National Museum (USNM).

2 ♀♀. USNM 143848. Cruise Dodo VI, stn 49, 1-m net, 0-200 m wire out (MWO); 20 Aug. 1964, 1445-1500 h; 10°19′N, 53°11′E.

3 ♀♀. USNM 143849. Cruise Dodo VI, stn 47, 1-m net, 0-200 MWO; 19 Aug. 1964, 1825-1840 h; 8°53′N, 53°09′E.

1 ♀. USNM 143850. Cruise Scot (TO58-1), stn 35, 1-m net, surface; 7 May 1958, 0343 h; 9°45′N, 96°04′W.

Remarks: Dana's (1849, p. 18, 19) first locality given for *attenuatus* is from the vicinity of the Kingsmill (= Gilbert) Islands in the western Pacific (13 April 1841). Other U.S. Exploring Expedition localities include the China Sea at about lat. 5° to 10°N (15 February 1842) and the Sulu Sea (2 February and 2 March 1842). All of these localities lie in Indo-Pacific tropical waters, the biogeographical zone and the geographical region that yielded most of the records of *attenuatus* s.s. Moreover, Dana's figures (1853, Figure 2d, e) of *attenuatus*, while crude emphasize a short wide-angled forehead characteristic of the tropical population.

Vervoort (1946) noted two morphological kinds of *attenuatus* s.l. in *Snellius* collections, and his illustration (Figure 7c) probably refers to *attenuatus* s.s.

Sewell's (1947) description of *pseudattenuatus* shows a pattern of integumental organs ascribable to the tropical species *attenuatus* s.s. His illustration of *attenuatus* (1947, Text Figure 7B) appears on the basis of an incomplete account of integumental organs and the forehead to be referrable to *sewelli* described below.
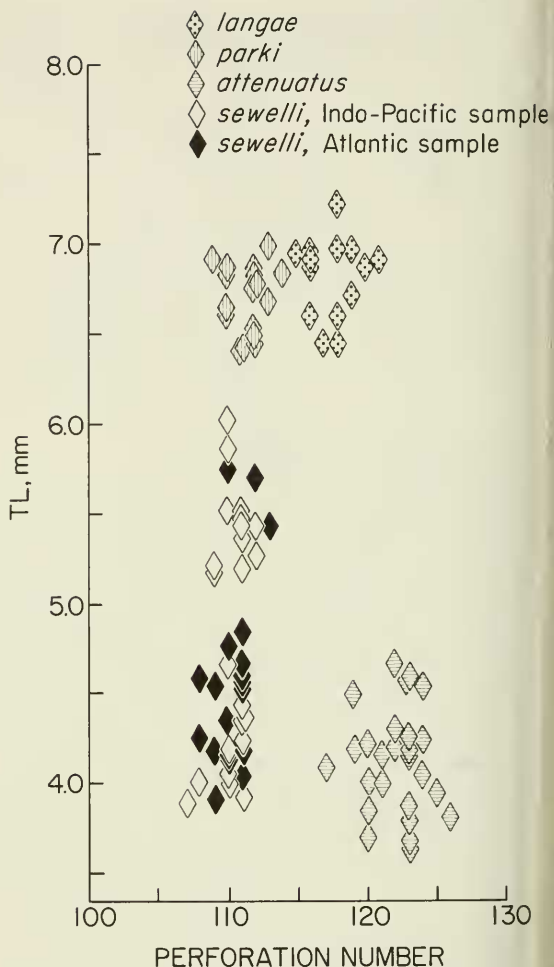

FIGURE 16.—The attenuatus group of *Eucalanus*. Perforation number plotted against total length (TL) in adult females comprising the pooled samples.

Brodsky's (1962) description of *pseudattenuatus* may be based on *attenuatus* s.s., but the figures fail to provide adequate details of the forehead and the absence of information on dorsal integumental organs on ThIII and ThIV leave the issue open.

Eucalanus sewelli, n. sp.
(Figures 1r, 15c, 18b-d, o, r)

E. *attenuatus:* Vervoort 1946, p. 95-103 (pars), Figs. 7d-f; Sewell, 1947, p. 39, Text-fig. 7B; Brodsky 1962, p. 113, Fig. 14.
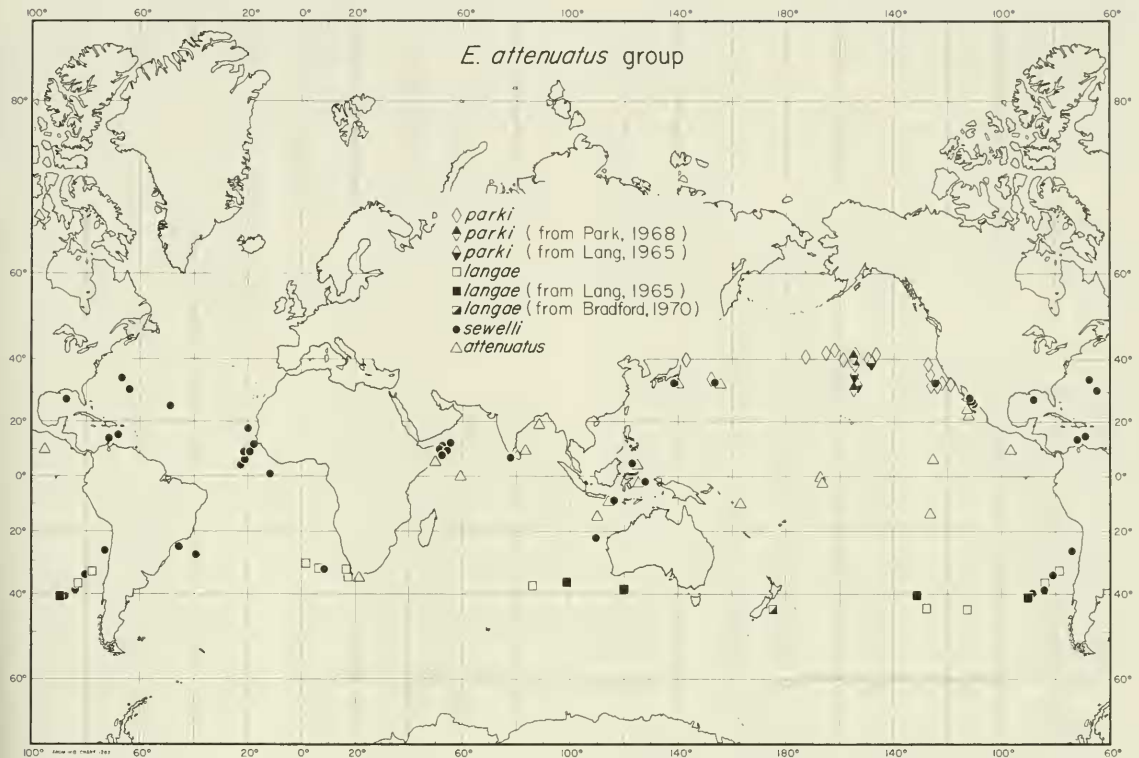
FIGURE 17.—Geographical localities of the species in the attenuatus group. All identifications except those of Park (1968) and Bradford (1970) verified by examination of integumental organs.

Diagnosis: Adult female with mandibular basis bearing two setae as in *attenuatus*. Differs from *attenuatus* in designated sites on ThIII and ThIV, each of which lacks the two pairs of tergal sites enclosed by the outer arc of six tergal sites (Figure 15c). Genital segment lacking integumental organs. Abd.IV-V with two transverse tergal rows and lacking pleural sites (Figure 15c).

Adult male: Tergal sites on ThIII and ThIV as in female. Abd.II lacking dorsal integumental organs (Figure 18i). Mandibular basis with two setae.

Additional description: Adult female with forehead more strongly attenuated and longer than that in *attenuatus* (Figure 15c), apex usually curving weakly ventrad (Figure 18c). In relatively eutrophic regions of the Indo-Pacific *attenuatus* and *sewelli* may co-occur and

resemble one another in size and general morphology, but differences in integumental organs persist. In strongly eutrophic tropical regions *sewelli* may exceed 6 mm in TL and exhibit a more prominent conical forehead with rounded apex (Figure 18d). Male with fifth pair of legs as in *attenuatus* (Figure 18o, r).

Total length: Adult female: range 3.89 to 6.10 mm, mean = 4.720 mm, s = 0.6350, N = 43 (Figure 16).

Adult male: range 2.89 to 4.58 mm, mean = 3.195 mm, s = 0.4680, N = 14. Specimens selected at random from localities listed in Table 1.

Geographical distribution: Verified localities (Figure 17) indicate a circumglobal range in eutrophic tropical and subtropical waters extending to the subtropical convergences.
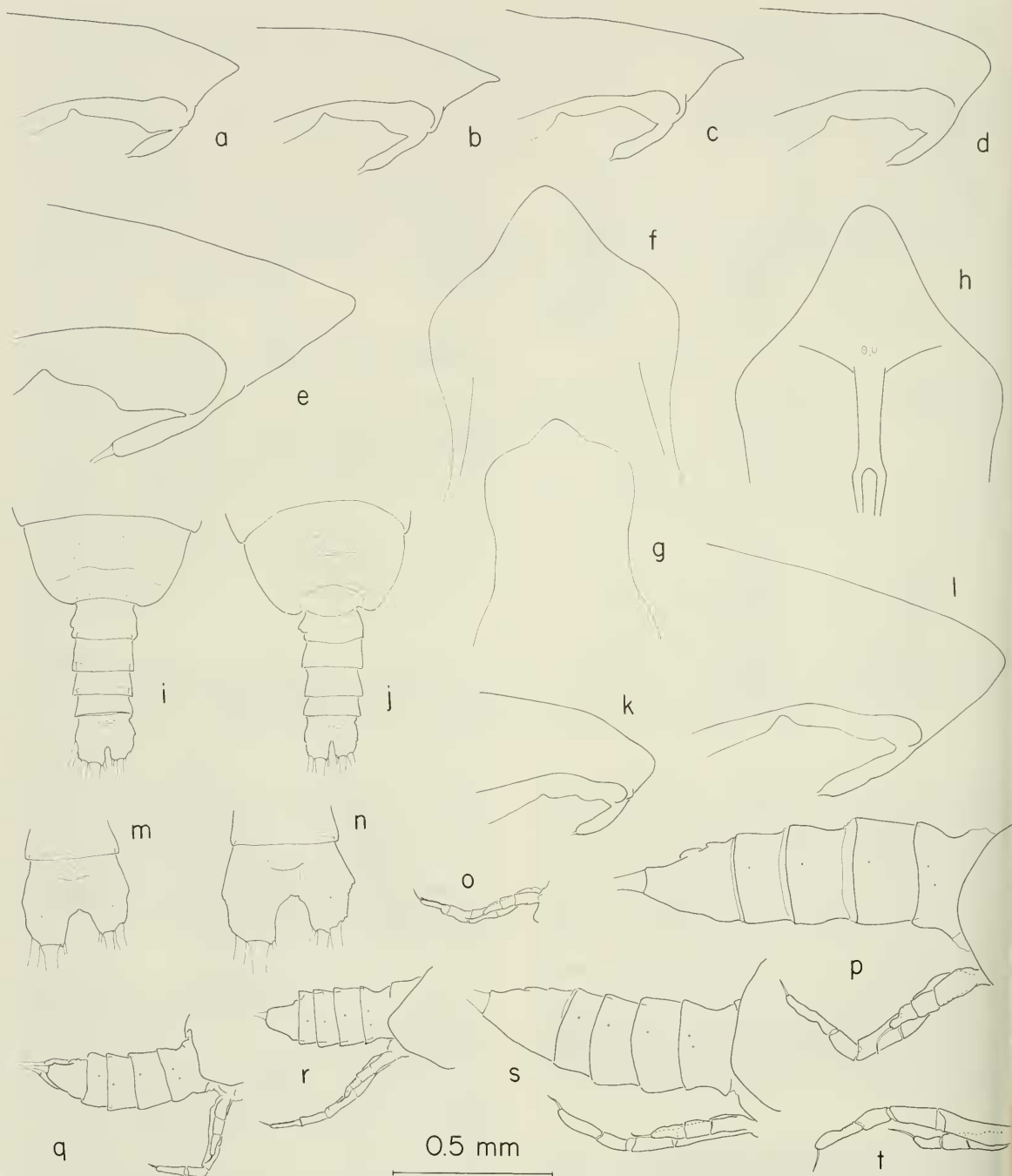
993

FIGURE 18.—Anterior portion of head, lateral view, female; **a.** *Eucalanus attenuatus* (EQUAPAC S 21); **b.** *sewelli* (*Alaska* 5-9); **c.** *sewelli* (Naga S11A 61-198); **d.** *sewelli* (CalCOFI 5708 144.G15); **e.** *parki* (Boreas 19). Anterior portion of head, dorsal view, male; **f.** *parki* (Zetes 14); **g.** *attenuatus* (EQUAPAC S 21). Anterior of head, ventral view, female; **h.** *langae* (Lusiad 14). ThIV-V and abdomen, dorsal view, male; **i.** *sewelli* (CalCOFI 5708 144.G15); **j.** *attenuatus* (EQUAPAC S 21). Anterior portion of head, lateral view, male; **k.** *attenuatus* (EQUAPAC S 21); **l.** *parki* (Zetes 14). Anal segment and fused furcal rami, dorsal view, male; **m.** *parki* (Zetes 14); **n.** *attenuatus* (Monsoon 24). Fifth pair of legs, male, right lateral view; **o.** *sewelli* (CalCOFI 5708 144.G15); **p.** *langae* (Lusiad VII MWT 19); **q.** *attenuatus* (EQUAPAC S 21); **p.** *sewelli* (*Alaska* 5-9); **s.** *parki* (CalCOFI 5804 80.130); left lateral view; **t.** *parki* (Boreas 19). Positions for stations mentioned are listed in Snyder and Fleminger (1965, 1972).

Types and type locality: Holotype: ♀. USNM 143844. Cruise Downwind, stn 23a, 45-cm net, 0-352 m; 19 Oct. 1957, 0000-0100 h; 38°46'S, 83°20'W.

Reference: 3 ♀♀. USNM 143845. Cruise Downwind, stn 28, 1-m net, 0-283 m; 31 Dec. 1957, 0520-0542 h; 27°08.5'S, 72°02'W.

3 ♀♀. USNM 143846. Cruise Atlantis II-13, stn 8, ¾-m net, depth? 5 Oct. 1964, 1410-1435 h; 41°26'N, 55°45'W.

1 ♀. USNM 143847. Cruise Dodo VI, stn 55, 1-m net, 0-200 MWO; 22 Aug. 1964, 1845-1858 h; 10°14'N, 51°19'E.

Remarks: Brodsky's (1962, p. 113) record of (?) *attenuatus* appears from his illustration (Figure 14) and the locality off northern Japan to be referable to *sewelli*. Other records that appear to be assignable to *sewelli* include Tanaka (1956, p. 266, Figure 4a), Ramírez (1969), and Roe (1972). This species is named to honor R. B. Seymour Sewell who among his many significant contributions to the copepod literature inspired study of their integumental organs and directed attention to the complexity existing in the attenuatus group.

Eucalanus parki, n. sp.
(Figures 1s, 15a, 18e, f, 1, m s, t)

E. attenuatus: Park 1968, p. 533, Pl. 1, Figs. 16, 17, Pl. 2, Figs. 1-16, Pl. 3, Figs. 1-13, large form only.

Diagnosis: Adult female: Mandibular basis with four setae. Sites of integumental organs similar to those of *sewelli* except for presence of one medial tergal site on both the genital segment and on Abd.III, one or more pleural sites on Abd.IV-V, and only one transverse tergal row on Abd.IV-V (Figure 15a).

Adult male: Forehead prominent, protruding as an elongate triangle about twice as far beyond base of rostrum as in *sewelli* and *attenuatus* (Figure 18f). Integumental organs on cephalosome and thorax as in female; Abd.II with or without one tergal site (in 11 specimens, 6 with and 5 without). Mandibular basis usually with four setae, one specimen in 11 with three setae.

Additional description: Adult female with conical forehead and rounded apex as in Figure 18e, differs from typical acutely pointed forehead of *sewelli.*

Total length: Adult female: range 6.40 to 7.17 mm, mean = 6.744 mm, s = 0.1982, N = 18 (Figure 16).

Adult male: range 5.20 to 5.96 mm, mean = 5.620 mm, s = 0.2380, N = 10. Localities of specimens listed in Table 1, pooled sample represents all adults on hand.

Geographical distribution: All records (Figure 17) are from the North Pacific Ocean. Most fall within the Transition zone (Brinton, 1962, p. 202) but a number also appear along long. 155°W extending south to lat. 32°N, following the line of division between western and eastern North Pacific Central Water (Sverdrup, Fleming, and Johnson, 1942, Figure 209A) which is supported by the relative elevation of the isotherms in the upper 200 m of the mid-latitudes in the North Pacific relative to those of the South Pacific (Reid, 1965, Figure 2).

Types and type locality: Holotype: ♀. USNM 143841. Cruise Norpac H5508, stn 24-42, 1-m net, 0-200 MWO; 21 Aug. 1955; 1556-1610 PST; 40°26'N, 146°37'W.

Reference: 1 ♀, specimen no. 2. USNM 143842. Cruise Norpac H5508, stn 24 (up), 1-m net, 0-200 MWO; 25 Aug. 1955, 1620 PST; 42°17'N, 146°16'W.

1 ♀, specimen no. 1. USNM 143843. Cruise Norpac H5508, stn 25 (up), 1-m net, 0-200 MWO; 25 Aug. 1955, 1816-1831 PST; 42°17'N, 150°00'W.

Remarks: Large forms of *attenuatus* s.l. have been noted from the North Pacific by several authors (e.g., Tanaka, 1956, p. 266, Figure 4b; Lang, 1965 Park, 1968). Park (1968) fully appreciating its distinctiveness described it in detail. He relinquished his original intention of naming it as a distinct species upon my recommendation, which was based on the apparently extensive variability generally thought to prevail in *Eucalanus.* At that time there was no reliable basis for distinguishing genetic from phenetic variation and reliable capture records

were insufficient to provide an indication of biogeographical affinities. It is a great pleasure to name this species for TaiSoo Park in recognition of his acumen and farsightedness in judging copepod systematics.

Eucalanus langae, n. sp.
(Figures 1t, 15b, 18h, p)

E. attenuatus: Bradford 1970, p. 353, Figs. 6-9.

Diagnosis: Adult female: Closely resembling *parki* in size and appearance including the occurrence of four setae on the mandibular basis. Integumental organs as in *parki* except for significant increase in abdomen (Figure 15b). Genital segment and Abd.III each with two tergal sites. Anal segment (Abd.IV-V) with two transverse rows of tergal sites as well as more regularly occupied pleural sites occurring in copepodid stage V and in adults (Figure 19, Table 5), the mean total number being about twice that of *parki.*
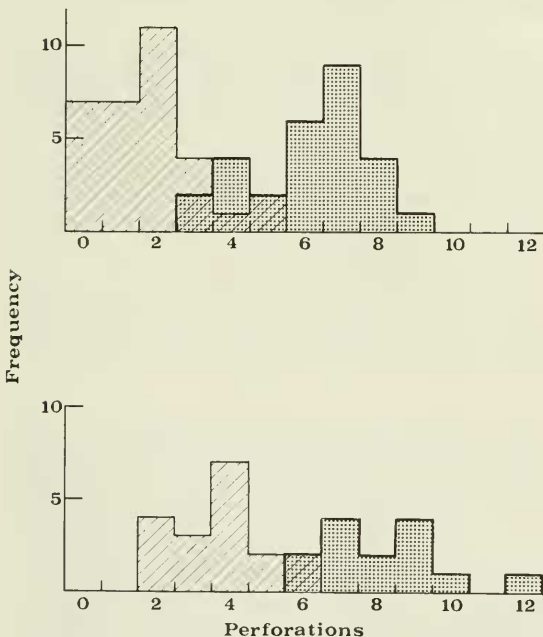

FIGURE 19.—Frequency distribution of the total number of perforations on the anal segment (Abd.IV-V) in stage V female copepodids above and in adult females below. Diagonal hashing represents *Eucalanus parki,* dotted area represents *E. langae.*

Additional description: Adult male: Integumental organs of cephalosome and thorax as in female; Abd.II with two tergal sites as in genital segment of female.

Total length: Adult female: range 6.44 to 7.22 mm, mean = 6.847 mm, $s = 0.2235$, $N = 14$ (Figure 16).
Adult male: 6.12 mm and 6.59 mm. Localities of specimens given in Table 1.

Geographical distribution: Available records (Figure 17) indicate that *langae* is a resident of the circumglobal Transition zone in the Southern Hemisphere.

Types and type locality: Holotype: ♀. USNM 143839. Cruise Lusiad VII, stn 14, Isaacs-Kidd midwater trawl; 0-3,400 m; 6 June 1963, 1530-2300 h; 32°30′S, 9°04′E to 32°24′S, 8°25′E.
Reference: 2 ♀♀, specimens no. 4 and 6. USNM 143840. Cruise Monsoon, stn 18, Isaacs-Kidd midwater trawl; 0-2,723 m; 11 Mar. 1961, 2046-0303 h; 25°52′S, 155°44′W to 25°40′S, 155°34′W.

Remarks: Lang (1965) found specimens of this species at several Monsoon and Downwind stations (Figure 17) and noted their resemblance to their North Pacific temperate cognate. Bradford (1970) also noted this similarity in recording it from off the Kaikoura Peninsula, New Zealand, and referring to Tanaka's (1956) mention of a large *attenuatus* s.l. off Japan.
Though data on designated sites are lacking for Bradford's specimens, the probability that they are referable to *langae* is sufficiently great to include them under the species without reservation.
Assignment of the sibling populations *langae* and *parki* to separate species is based on two lines of evidence: 1) significant differences in designated sites involving abdominal segments that undergo modification with sexual maturation (Table 5, Figure 19); 2) apparent restriction of each population to temperate zones in opposite hemispheres (Figure 17).
Although data on actual depth distribution are unavailable for either species, most of the

TABLE 5.—Number of perforations on anal segment of *parki* and *langae* in copepodid stage V and adult females of *Eucalanus*.

Species	Range	$\bar{x}$	s	N	t	P
parki: stage ♀	0-5	1.75	1.4368	32		
adult ♀	2-6	3.7222	1.2744	18		
langae: stage V ♀	3-9	6.1428	1.6036	28		
adult ♀	6-12	8.1428	1.6576	14		
Comparison of sample means of female specimens						
parki stage V and adult ♀				50	4.85	<0.001
langae stage V and adult ♀				42	3.76	<0.001
stage V: *parki* and *langae*				60	11.193	<0.001
adults: *parki* and *langae*				32	8.55	<0.001

records of *langae* and *parki* (Table 1) are based on relatively shallow tows with open nets from 300 m or less to the surface. Following the shortest prevailing surface circulation in the Pacific Ocean, shallow water passage from the temperate zone of one hemisphere to that of the other is at least 9,000 miles long. It would begin necessarily in the eastern boundary currents and continue in the equatorial circulation where crossover to the succeeding western boundary current in the opposite hemisphere might occur. Assuming a high rate of 1 knot and an unrealistic expectation of continuous and direct transport would require a transit time exceeding 1 yr.

Among my unpublished records of *attenuatus* s.l. neither *langae*- nor *parki*-like individuals of any copepodid stage appear in the equatorial localities (cf. Fleminger and Hulsemann, 1973, for geographical distribution of samples that have been examined for *Eucalanus*). Moreover, no specimens that might be attributable to *langae* or *parki* on the basis of unusually large size appear among the published records of *attenuatus* s.l. collected from the vicinity of the Pacific's equatorial circulation.

Transhemispheric passage at subsurface depths would be at transport rates that are probably an order of magnitude less than surface transport. Evidence of tropical submergence by *attenuatus* s.l. is lacking, however, despite widespread studies on the vertical distribution of copepods in the upper 500 m of the Pacific. Also, *attenuatus* s.l. appears to be a fine particle filter-feeder (Mullin, 1966; Samyshev, 1970) and therefore not a likely candidate to survive deep submergence to meso-

or bathypelagic depths for periods of one or more years. In the light of this background the relatively small but constant morphological differences and an apparent allopatry, maintained by the formidable barrier of the tropical and subtropical zones separating the ranges of *parki* and *langae*, provide compelling reasons for treating the two biantitropical (Brinton, 1962) populations as separate species.

If *langae* could survive transport to temperate waters of the Northern Hemisphere it could be expected to appear in the North Atlantic Drift. Despite the great intensity of study on oceanic copepods of the North Atlantic no "giant" *attenuatus* s.l. forms have been noted from the region. With (1915, p. 52-53, Pl. 1, Figure 6a-c, Text figure 10a-e) reports several large *attenuatus* s.l. stage V copepodids (♀ = 5.18 mm, ♂ = 5.0 mm) collected at two North Atlantic localities lying roughly between Iceland and Scotland. With notes that "The structure of the mouth appendages . . . scarcely show differences of any importance from Giesbrecht's description . . .". Thus it seems likely that the mandibular basis in his specimens bore two setae as in *sewelli*, a species that reaches a length in accord with With's measurements (Figure 16 and see p. 993 above). The absence of other reports of large *attenuatus* s.l. in excess of 6 mm in TL from the North Atlantic even at considerable depths (e.g., Roe, 1972) further substantiates the lack of a North Atlantic temperate cognate of *parki* and *langae*.

The species is named for Bui Thi Lang to acknowledge her discovery (1965) of morphological and geographical complexity in *attenuatus* s.l.

KEY TO THE SPECIES OF
EUCALANUS

(Adult Females Only)

Based on integumental organs, all sites are tergal unless specified otherwise.

1. Mxp with four or more pairs of sites; ThIII and IV lacking single middorsal site between anterolateral hair sensilla; ThIV lacking paired sites lying outside of dorsal quadrangle of hair sensilla 2

   Mxp usually with two pairs of sites; ThIII and IV with single middorsal site lying between anterior two hair sensilla; ThIV with one pair of sites lateral to quadrangle formed by four hair sensilla 3

2. Mx1 and Mx2 with total of 10 sites forming a rectangle and arranged anterior to posterior in two bilateral sets of one pair, one single and one pair of sites; ThII and III in lateral view with three sites, Abd.IV-V with at least three tergal sites .... attenuatus group, 4

   Mx1 and Mx2 sites vary from 8 to 18 in number, not arranged in rectangle pattern, posterior sets more lateral than anterior sets; ThII and III with one or two lateral sites; Abd.I-II with at least two tergal perforations .... elongatus group, 5

3. ThIII and IV with one medial site in tergal arc formed by the tergal sites .... subtenuis group, 6

   ThIII and IV with two medial sites in the arc formed by the tergal sites .... pileatus group, 7

4. A. Abd.III with tergal site .... B

   Abd.III lacking tergal site C

B. Abd.I-II usually with one site, Abd.IV-V with three tergal and one pleural site ...... *parki*

   Abd.I-II usually with two sites, Abd.IV-V with at least four tergal and three pleural sites .... *langae*

C. Abd.I-II lacking tergal sites, Abd.IV-V usually with five tergal and zero pleural sites .... *sewelli*

   Abd.I-II with two tergal sites, Abd.IV-V with three tergal, usually two or more pleural sites .... *attenuatus*

5. A. ThII and III with a pair of sites anterolateral to arc formed by tergal sites; Mx1 and Mx2 with at least 16 sites .... B

   ThII and III lacking a pair of sites anterolateral to arc formed by tergal sites, Mx1 and Mx2 with 12 or fewer sites .... D

B. ThI and II each with seven tergal sites; Abd.I-II with three tergal sites .... *hyalinus*

   ThI with 13, ThII with nine tergal sites; Abd.I-II with four tergal sites C

C. Mandibular basis with one seta .... *californicus*

   Mandibular basis with three setae .... *bungii*

D. A1 somite with sets of eight and four sites; Mnd somite with six sites; ThV with three sites; Abd.I-II with two sites, Abd.III and IV lacking tergal sites, Abd.IV lacking pleural sites .. *inermis*

   A1 somite with sets of six and two sites; Mnd somite with two to four sites; ThV

with four or more sites;
Abd.I-II with four or more
sites; Abd.III and IV with
two or more sites; Abd.IV
with one pleural site . . . .   *elongatus*

6. A. Mx2 somite with two or
   more pairs of sites; ThI
   with seven or more sites;
   ThII and III with one
   asymmetrical site within
   arc of hair sensilla on left
   of midline; Abd.I-II with
   two sites . . . .   B

   Mx2 somite lacking sites;
   ThI with three sites; ThII
   and III lacking sites with-
   in dorsal arc of hair sensil-
   la; Avd.I-II with up to
   one site   C

B. ThI with 15 sites; Mx1 so-
   mite with 10 sites includ-
   ing a medial set of four; A1
   somite with 10 sites includ-
   ing a posterior set of four;
   Mnd somite with eight sites .   *subtenuis*

   ThI with seven sites; Mx1
   somite lacking four medial
   sites; A1 somite lacking
   four posterior sites; Mnd
   somite with four to six
   sites . . . .   *mucronatus*

C. ThII and III with three
   pleural sites, Abd.IV-V
   with three tergal sites . . . . .   *monachus*

   ThII and III with two
   pleural sites, Abd.IV-V
   with one tergal site . . . .   D

D. Mnd somite with six sites;
   Abd.I-II lacking tergal sites . .   *crassus*

   Mnd somite with four sites;
   Abd.I-II with one tergal
   site . . . .   *longiceps*

7. A. ThII and III with two pairs
   of pleural sites; Mx2 somite
   with two pairs of tergal
   sites; Abd.I-II with three

sites; Abd.III with two
sites . . . .   B

ThII and III with one pair
of pleural sites; Mx2 so-
mite lacking tergal sites;
Abd.I-II usually with one
site; Abd.III lacking tergal
sites . . . .   *pileatus*

B. Mx1 somite with two pairs
   of sites adjacent to the mid-
   line; Abd.IV-V with one
   site . . . .   *subcrassus*

   Mx1 somite with one pair
   of sites adjacent to the mid-
   line; Abd.IV-V with three
   sites . . . .   *dentatus*

USE OF INTEGUMENTAL ORGANS
IN STUDIES ON
GEOGRAPHICAL VARIATION

A relatively high degree of variability in
perforation number was noted for the circum-
global, broadly tropical species, *E. subtenuis*
(Table 4, Figures 9, 10). The conspicuous
variability was noticed after realization that
bilateral symmetry and arrangement in regular
patterns distinguishing species groups as well
as species is characteristic of integumental
organs. The variation suggested that these
organs are a promising source to search for
evidence of genetic variation in field-collected
planktonic populations. Thus to carry out a
pilot study of this possibility the original sam-
pling of *subtenuis* was supplemented by addi-
tional specimens sorted at random from zoo-
plankton samples selected to represent both
extreme and intermediate geographical loca-
tions within the known distribution in each
ocean (Figure 20). For each specimen pleural
perforations were tallied from both left and
right sides of the entire body and summed with
counts of the tergal perforations to obtain a
maximum estimate referred to as the perfora-
tion number (PN). TL was also measured
routinely using procedures described in the
section on Material and Methods. It should be
noted that no attempt was made to determine
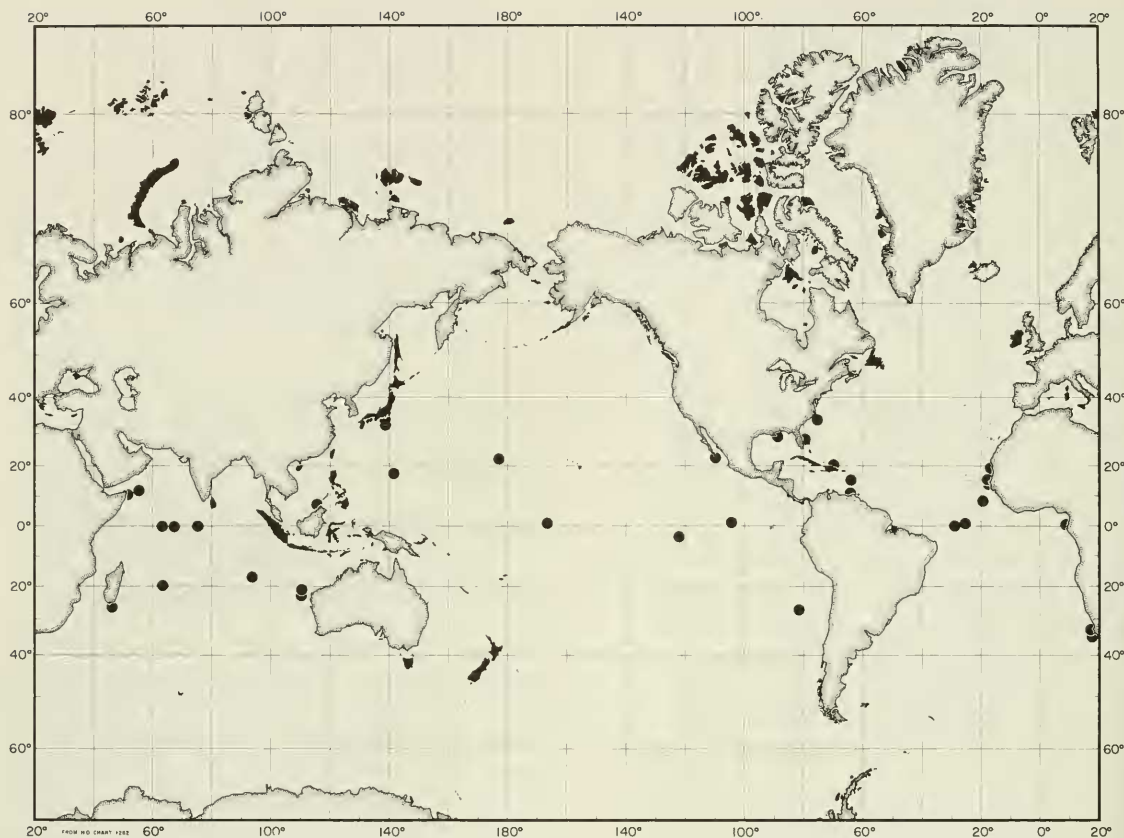the existence of geographical variation in any

FIGURE 20.—Geographical distribution of *Eucalanus subtenuis*. Localities shown based on records verified by analysis of integumental organs.

other morphological features of *subtenuis* except to confirm that in virtually all specimens from each ocean the mandibular basis bore three setae as found by Fukase (1957).

The data were first examined by pooling the samples from each ocean and comparing the mean number of perforations between oceans. Differences between the pooled samples proved to be highly significant (Table 6), and the mean PN values show a pronounced geographical trend. The lowest mean was obtained from the Pacific Ocean specimens and the highest from the Atlantic Ocean specimens. The pooled sample from the Indian Ocean yielded a mean PN virtually midway between the other two.

The gross indication of clinal variation suggested further consideration at a finer scale.

The PN counts of *subtenuis* were regrouped by geographical source of the specimens in units of 60° of longitude and compared in terms of frequency distribution and mean PN per geographical segment (Figure 21). Grouped samples falling within the hydrographic limits of any one ocean do not differ significantly (Table 7) and serve to emphasize the stepped or discontinuous pattern of the means from the different oceans. The range shown by PN in the two geographical segments between long. 30°E and 150°E (Indian Ocean and westernmost Pacific Ocean) spans the apparent differences in the distribution of PN in the Pacific and Atlantic samples (Figure 21). Thus the Indian Ocean population would appear to be the one genetically and geographically intermediate in

TABLE 6.—Total number (PN) of perforations in samples of *Eucalanus subtenuis* from different oceans.

Sample	Range	$\bar{x}$	s	s^2	N	t	P
Pacific Ocean	114-135	123.6388	4.9750	24.7506	36		
Indian Ocean	119-139	130.0416	4.9911	24.9111	24		
Atlantic Ocean	125-141	134.8400	3.2598	10.6263	50		
Comparison of differences between mean number (Student's t - test)							
Pacific : Indian					60	4.877	<0.001
Indian : Atlantic					74	4.98	<0.001
Atlantic : Indian-Pacific combined					110	9.37	<0.001

position to those of the Pacific and Atlantic populations, a pattern consistent with the prevailing surface circulations of equatorial and western boundary currents.

When the various sets of perforations are analyzed separately, however, the resemblance of the variation to either a zone of intergradation or a stepped cline disappears. The designat-

ed sites in *E. subtenuis* fall into 26 tergal and 13 pleural sets based on the scheme described above (Figures 5, 7). More than half of these sets show zero or negligible variability, i.e., typical perforations were observed at these sites in virtually all of the specimens. Most of the variation was in fact concentrated in only nine sets of designated sites (Figure 22a, b).
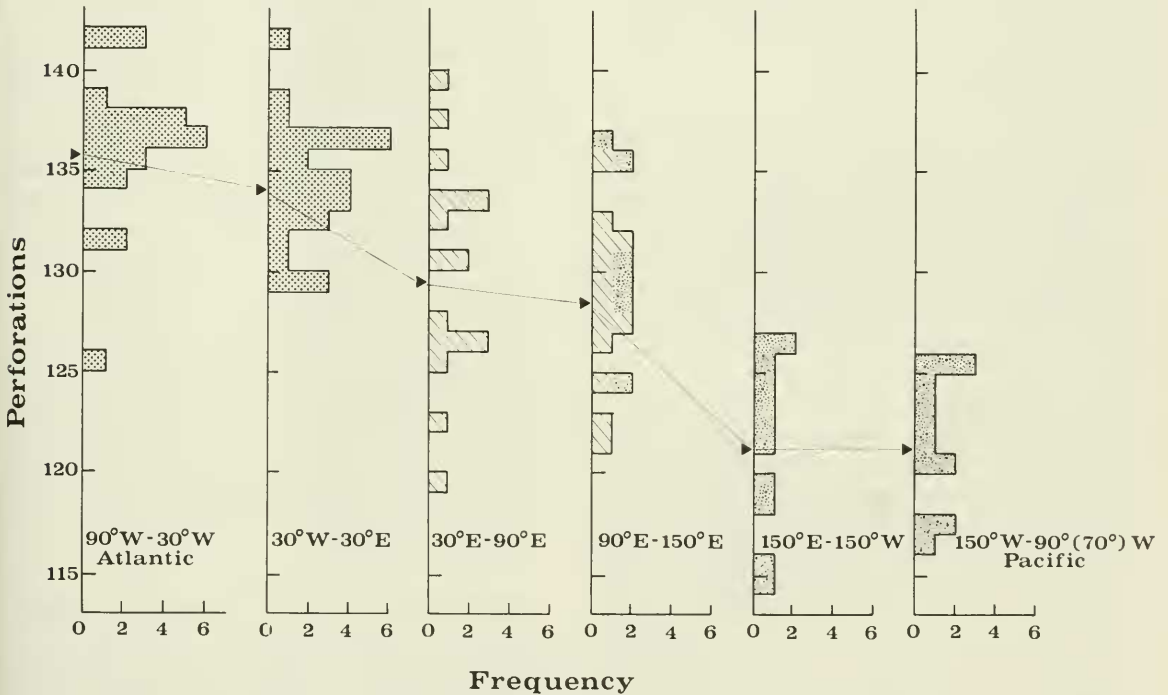

FIGURE 21.—Frequency distribution of total number (PN) of perforations per specimen in samples of adult females of *Eucalanus subtenuis* collected within 60° segments of longitude. Uniform large spot shading represents specimens collected at localities in the Atlantic Ocean; obliquely ruled shading represents specimens collected at localities in the Indian Ocean; irregular finely dotted shading represents specimens collected at localities in the Pacific Ocean. Differences between the means in the second and third histograms and the fourth and fifth histograms counting from the left are highly signifiicant (*t*-test, Table 7). Black triangle indicates position of mean PN within geographical segment. All specimens selected at random from zooplankton samples located in various sectors of the *subtenuis* range (Figure 20).

TABLE 7.—Comparison by Student's t-test of mean TN values of samples of adult female *subtenuis* grouped regionally as in Figure 21 in segments of 60° of longitude.

Regional segments (longitude)	$N_1 + N_2$	$\bar{x}$	t	P
90°-30°W : 30°W-30°E	52	135.74 : 134.00	1.99	$<0.1 \; P >0.05$
30°W-30°E : 30°-90°E	45	134.00 : 129.56	3.59	<0.001
30°-90°E : 90°-150°E	35	129.56 : 128.68	0.54	$<0.6 \; P >0.5$
90°-150°E : 150°E-150°W	30	128.68 : 121.18	5.623	<0.001
150°E-150°W : 150°-90°(70°)W	23	121.18 : 121.25	0.064	>0.9
150°-90°(70°)W : 90°-30°W	35	121.25 : 135.74	11.91	<0.001

The nine sets appear to vary independently of one another, some showing unusually high or low frequencies of absence in one or two of the three oceans. In some sets the frequency of absence in one ocean differs significantly from that elsewhere (Figure 22a, b; Table 8). Within each set perforations tend to be absent at similar frequencies. Genetic linkage is suggested by the similar deviations in the Pacific sample affecting the following sets: Mx1-T-a-l3, 4, r3, 4; Mxp-T-l1, 2, r1, 2; ThII-P-la1, ra1; ThIII-P-la1, ra1; and ThIV-P-la1, ra1.

Also unique to the Pacific sample is the more frequent occurrence of four perforations on the somite of the first maxilla (Mxl-T-d-l1, 2, r1, 2). The Indian Ocean sample is distinguished by a relatively infrequent appearance of the set of perforations on the somite of the second antenna (A2-T-a-l1, 2, r1, 2). The Atlantic sample shows relatively few absences on the Mx1 somite (Mx1-T-c-l1, 2, r1, 2) and on ThII (ThII-T-a-l2, 3, r2, 3).

In an individual specimen perforations are often absent in pairs rather than in full sets though right and left pairs in a set tend to show similar frequencies in the sample. Absences of peg and pore combinations are usually bilateral and affect both the right and left sides of a particular set. Absences of pairs consisting of a pit sensillum and a pore may be bilateral but more frequently affect only one side in a specimen. An appreciable portion of the variability in *subtenuis* emanates from losses among such tergal pairs occurring sequentially on the two maxillary somites. An individual specimen may show losses that alternate in successive sets from either left to right or the reverse. A noticeable trend in losses toward unbalanced symmetry was found only in the case of Mx1-T-b-l1, 2,

r1, 2. Indian and Atlantic samples showed more absences on the right side and Pacific samples had a higher frequency of absence on the left side, but the differences are significant (χ^2 test for homogeneity) only in the case of the Indian Ocean sample (Table 9). Critical examination for patterned variation among specimens using larger samples may prove to be especially useful for genetic studies on natural and laboratory populations of planktonic copepods.

Despite the relatively frequent absences, each of the 110 specimens of *subtenuis* comprising the combined global sample exhibited a representative perforation pattern permitting identification to species by this feature alone. Also noteworthy is the qualitative resemblance in characters distinguishing the geographical populations of *subtenuis* and differences separating *parki* from *langae*. As in *subtenuis* few perforations distinguish these allopatric temperate species of the attenuatus group from one another, and the sites involved are also restricted to a limited portion of the body (i.e., the abdomen and especially Abd.IV-V). The parallels emphasize the likelihood of appreciable genetic discontinuity separating Atlantic, Indian, and Pacific populations of *subtenuis* that deserves more intensive study.

SIZE AND PERFORATION NUMBER

The perforation number (PN), i.e., the number of designated sites in the species observed on each specimen is derived from a meristic complex of integumental organs. The two organ systems, sensilla and glandular pores, are arranged in serially homologous sets that are distributed on all body segments. Showing phylogenetic and species specific patterns, they
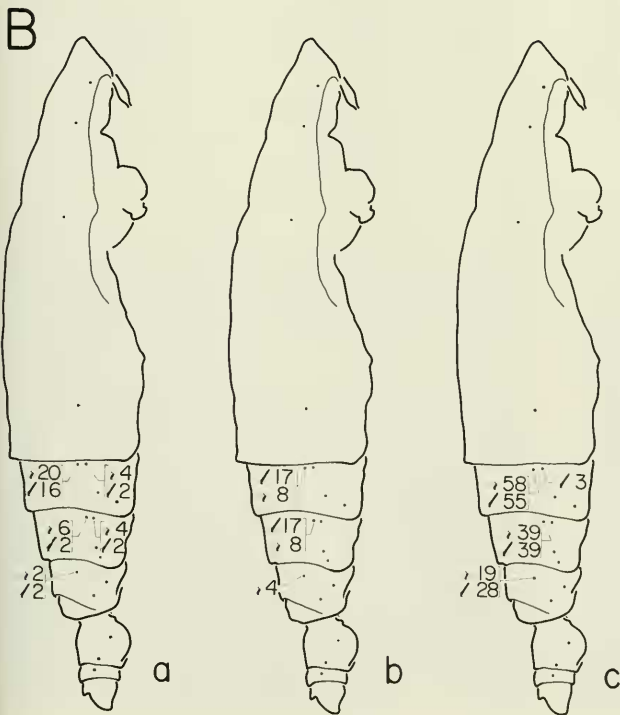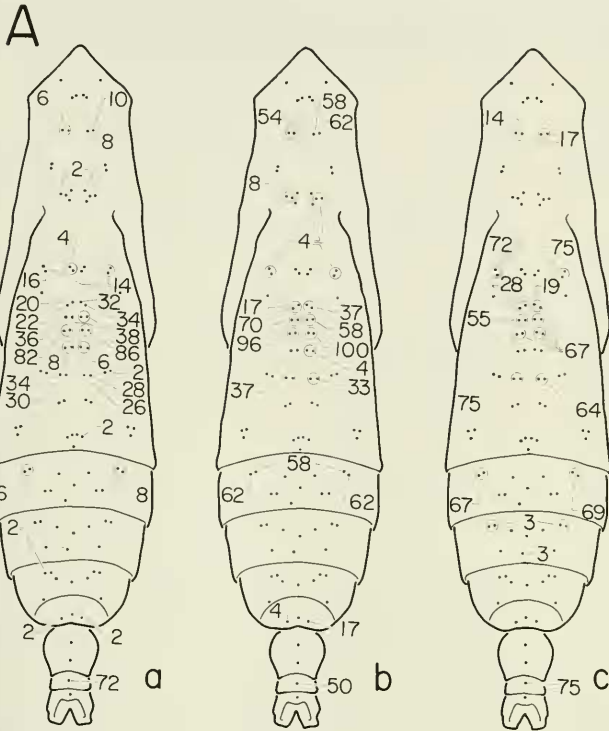
FIGURE 22.—Variation in the occurrence of perforations at designated sites in three regionally pooled samples of *Eucalanus subtenuis* adult females. Sampling localities shown in Figure 20 and geographical grouping based on significant differences between geographical regions shown in Table 7. From the left: Atlantic Ocean sample ($N = 50$), Indian Ocean sample ($N = 24$), Pacific Ocean sample ($N = 36$). Dots represent perforation sites typical of the species. Numbers represent percentage of specimens lacking a perforation at this site; open circles enclose pairs of sites showing the same frequency of absence. Absence of a number indicates perforation found in all specimens of the sample. Dorsal view top; right lateral view bottom.

TABLE 8.—X^2 test for homogeneity of frequency of absence of perforations from designated sites among geographically different samples of *Eucalanus subtenuis* adult females described in Figures 20 and 21.

Regional sample N	Frequency of absences			Atl., Ind., Pac. compared		Atl., Ind. compared		Atl., Pac. compared		Ind., Poc. compared		Largest source of X^2
	Atl. 50	Ind. 24	Pac. 36	X^2	P2d.f.	X^2	P1d.f.	X^2	P1d.f.	X^2	P1d.f.	
Designated sites (no.)												
A2-Ta Σl1,2;r1,2 (4 sites)	15	55	23	99.8	<0.001	89.2	<0.001	5.28	<0.025 P>0.01	44.6	<0.001	Indian
Mx1-Ta Σl3,4;r3,4 (4 sites)	29	4	106	179.9	<0.001	6.98	<0.01 P>0.005	122.2	<0.001	108.2	<0.001	Pacific
Mx1-Tc Σl1,2;r1,2 (4 sites)	75	62	88	27.5	<0.001	19.1	<0.001	18.7	<0.001	0.26	<0.75 P>0.5	Atlantic
Mx1-Td Σl1,2;r1,2 (4 sites)	168	94	96	39.3	<0.001	12.3	<0.001	14.1	<0.001	29.1	<0.001	Atlantic
Mxp-T Σl1,2;r1,2 (4 sites)	59	34	100	57.7	<0.001	1.0	<0.5 P>0.25	53.8	<0.001	27.1	<0.001	Pacific
ThII-Ta Σl2,3;r2,3 (4 sites)	14	58	98	156.2	<0.001	100.7	<0.001	142	<0.001	1.48	<0.25 P>0.1	Atlantic
ThII-Pr,l Σa1 (2 sites)	4	6	28	32.3	<0.001	~0.8	<0.5 P>0.25	22.2	<0.001	18.0	<0.001	Pacific
ThIII-Pr,l Σa1 (2 sites)	4	6	28	33.3	<0.001	3.7	<0.1 P>0.05	30.2	<0.001	8.3	<0.005 P>0.001	Pacific
ThIV-Pr,l Σa1 (2 sites)	2	1	17	26.0	<0.001	0	>0.9	18.7	<0.001	9.5	<0.005 P>0.001	Pacific
No. X^2 with $P \leq 0.5$				9		5		9		7		

are the unmistakable phenetic expression of the genotype.

Body size (TL) is a priori also under genetic control, and probably in copepods this control is rigorous (Brooks and Dodson, 1965; Brooks, 1968; Dodson, 1970; June and Carlson, 1971). However, it is known that in addition to selection pressures diet and temperature may strongly influence size determination (Coker, 1933; Deevey, 1960, 1964, 1966; Omori, 1970). A question of immediate concern is whether TL and PN may be sufficiently related to show similar phenetic patterns of variation.

Morphogenesis during the copepodite phase of ontogeny appears to affect PN in a simple predictable fashion. In general, copepodid stages III, IV, and V were found with the same number and arrangement of sites, segment by segment, as they appear in adults of the species with exceptions in abdominal segments as indicated above. The exceptions noted are restricted to ontogenetic modifications in the addition of abdominal segments and subsequent fusion of segments brought on by sexual maturation. Thus at least during the second half of ontogenesis integumental organs maintain numerical and distributional relationships during typical size increases associated with moulting; no observations are available for copepodite stages I and II. If a relationship exists between TL and PN it should be apparent from comparison of the two within a given onto-

TABLE 9.—Frequency of absence of perforations at a designated site in *Eucalanus subtenuis* (%).

Sample	Designated site: Mx1-T-6 left 1, 2	right 1, 2	X², 1d.f.	P
Pacific Ocean	28, 28	19, 19	~1.6	<0.25 P>0.2
Indian Ocean	17, 17	37, 37	5.28	<0.025 P>0.02
Atlantic Ocean	20, 20	32, 32	3.64	<0.1 P>0.05

TABLE 10.—Correlation coefficient (*r*) of TL and PN in adult females of *Eucalanus*. Original measurements shown graphically in Figures 10, 12, 14, 16.

Species	N	r	P
subtenuis:			
Atlantic	50	0.0241	>0.1
Indian	24	.1683	>0.1
Pacific	36	.3586	<0.05 P>0.02
mucronatus	20	.4743	<0.05 P>0.02
crassus	10	−.3477	>0.1
longiceps	12	−.3311	>0.1
monachus	17	−.5967	<0.02 P>0.01
pileatus	20	−.3556	>0.1
subcrassus	34	.1569	>0.1
dentatus	21	−.0543	>0.1
elongatus	19	−.0518	>0.1
hyalinus	25	.0831	>0.1
inermis	16	.2365	>0.1
bungii	15	−.0434	>0.1
californicus	22	.3241	>0.1
attenuatus	26	−.0498	>0.1
sewelli	43	.3446	<0.05 P>0.02
parki	17	.0407	>0.1
langae	14	.0565	>0.1

genetic stage. In making such comparisons, however, it should be recalled that considerations limited to the numerical value of PN is meaningful primarily within a species group. Between groups numerical differences in designated sites may not occur, but the species always differ in topographic arrangement of sets of perforations common to their respective group (Figures 9, 11, 13, 15).

Scatter diagrams of TL and PN (Figures 10, 12, 14, 16) show no common pattern of relationship among the 19 distinguishable populations (i.e., including the three geographical populations of *subtenuis*). Pearson's product-moment correlation coefficients were calculated for the available measurements of each population (Table 10). Eleven were positive correlations and eight were negative, a division indicative of the absence of a real relationship between TL and PN in the genus. Only four of the correlations depart significantly from zero (5% level): three are positive correlations and one is negative. All aspects considered, the four significant correlations, i.e., *subtenuis*, Pacific Ocean (+), *mucronatus* (+), *sewelli* (+), and *monachus* (−) are probably spurious. Thus, as a working hypothesis PN and TL may be considered to vary independently in adult female *Eucalanus*.

These data shed light on another vital question involving TL and PN, namely, whether in fact the two characters are related genetically. We may anticipate that such a relationship would be apparent by the correlation of the two characters in each species group.

Figures 10, 12, 14, and 16 in fact clearly show the absence of uniformity in the relationship of TL and PN across the genus. We find that each group presents a different pattern of relationship between TL and PN.

It would be of considerable interest to know if PN relates to geographical overlap in the breeding range of species of the same species group. Another related question of ecological significance is whether TL varies with the extent to which the range of a species falls outside of the ecological or biogeographic regions typically occupied by the species group.

REMARKS ON THE FUNCTION OF INTEGUMENTAL ORGANS IN *EUCALANUS*

With so few available retinal cells (Vaissière, 1961; Fahrenbach, 1962, 1964; Park, 1966), copepods must locate appropriate sexual partners, couple, and accomplish spermatophore transfer and attachment in the apparent absence of visual contact with the environment. In nature the available methods appear to be eminently successful in preventing hybrid pairing and in ensuring functional placement of the spermatophore's discharge canal on the female genital pore (Fleminger, 1967; Frost and Fleminger, 1968). External chemical and mechanical receptor-effector systems among the Crustacea appear sufficiently diverse to provide adequate non-visual channels mediating the exchange of information required by a relatively complex and efficient, instinctive mating behavior. As in

terrestrial arthropods microanatomical studies on copepods (Lowe, 1935; Fahrenbach, 1962; Park, 1966) reveal a highly organized central nervous system, one that supports innervated integumental sensilla and glands distributed symmetrically over the body. The receptors may monitor the environment, and the effectors may release information in response to appropriate stimulators.

Among semispecies, i.e., somewhat differentiated populations of a superspecies (Mayr, 1970), the primary reproductive barrier is extrinsic inasmuch as potential hybridizers lack access to one another. Assuming no significant contact since the inception of allopatry, intrinsic reproductive barriers, i.e., prezygotic mechanisms, if any, are untested and probably imperfect or nonexistent. Similar populations of recent common ancestry newly brought together through the expansion of ranges are likely to interact unfavorably across a spectrum of fundamental organismic processes and thereby experience pronounced selection pressures. When sympatry replaces allopatry among sets of semispecies hybridization is often intense in the area of geographical overlap (Remington, 1968; Rising, 1970).

The only stabilizing alternatives for such interacting populations are: 1) elimination of one or both; 2) genetic displacement; or 3) coalescence. Alternatives 1 and 2 will prevail if, in general, hybrid offspring are less fit and at a selective disadvantage and only postzygotic barriers are available. Development of increased efficiency of prezygotic barriers will be at a premium and the rate of their development and distribution will be a function of the rate of interactions and the mobility of the populations. According to MacArthur and Wilson (1967) a computer model by Bossert has indicated that full displacement is achieved rapidly and, under ideal conditions, equilibrium may be achieved in as few as 10 generations.

As seen in each of the species groups of *Eucalanus*, differences in the integumental organs between species groups include features common to all members and those common to members comprising the group. Within a group differences tend to occur on or near the genital segment. Moreover, there is a general trend for differences to be more pronounced in the populations whose distributions are most extensive and bring them into contact with the largest number of other members within the species group. Thus, the pattern of integumental organs in *Eucalanus* show configurations that appear to have been shaped by character displacement (Brown and Wilson, 1956) in the broadest sense or what some (Blair, 1963; Littlejohn, 1965) have referred to as reinforcement. If so, integumental organs in copepods may play a significant role in the mating process.

CONCLUSIONS

1. This study provides unique and compelling evidence of the extensive information content applicable to systematics, phylogenetics, evolution, and population biology present in the integumental sensory and effector organs of planktonic copepods.

2. Integumental organs appearing on the body segments in *Eucalanus* are distributed in bilaterally symmetrical, serially homologous patterns that appear in both dorsal (tergal) and lateral (pleural) sets corresponding to the somites of the body. The organs fall into two basic groups: a) receptors that appear as hairs, pegs, or pits and b) integumental glands that communicate with pores on the surface of the exoskeleton. Within the set of a somite each designated site is constant in position and in morphological type of organ relative to the others comprising the set.

3. Analysis and survey of the gross morphology, distribution, and variation of these integumental organs was facilitated by a combination of techniques including a) digestion of internal tissues and intensive staining for light microscopy, b) clearing and integumental staining of intact specimens for light microscopy, and c) scanning electron microscopy. Processing of relatively large numbers of specimens was accomplished most efficiently using method a.

4. Comparative survey of integumental organs in 17 species recognized in this study as comprising the genus *Eucalanus* indicated that the numbers and arrangement of these structures reflect generic similarities, species group similarities, and individual species patterns, all

species but one pair being sufficiently distinctive in number and arrangement to be identifiable solely on the basis of integumental organs. Species grouped on the basis of integumental organs concur with groupings that utilize the seminal receptacle, segmentation of the abdomen and structure of the male fifth legs. In general, variation was negligible; about 80% of the sites in each species was observed in all specimens examined and an additional 10% appeared in from 80 to 99% of the specimens. The mean number of organs observed in samples of each population ranged from a low of 83 to a high of 135 in a combined total of 448 randomly selected specimens representing the 17 species in the genus.

5. Comparison of geographical relationships and number of integumental organs within each species group indicates that the species with the broadest geographical range is also the one with the most distinctive number or arrangement of integumental organs especially with respect to organs on the genital segment. The combination of species specificity, phylogenetic relationships, and geographical patterns associated with numbers and arrangement of organs indicate that the organs may function in prezygotic mating barriers within the genus.

6. Comparison of total length and number of integumental organs indicates that the two features are unrelated.

7. Variation in integumental organs in the circumglobal broadly tropical species *E. subtenuis* was found to have a strong geographical pattern indicating limited gene flow between the populations of the Eastern Tropical Pacific, the Indo-West Pacific, and the Atlantic Ocean. Some sets of organs were found to vary independently; others appeared to vary similarly providing evidence that the genetic control is complex. Their responses to selection pressures appear to vary sufficiently to warrant detailed study of *subtenuis* in relation to its closest cognate, *mucronatus*, within and outside of their region of co-occurrence.

8. Limited examination of males and copepodid stages III to V indicate that the integumental organs appear in the same numbers and arrangements that characterize the adult female

except for structures that have not yet completed sexual maturation or are sexually dimorphic.

9. The attenuatus complex is revised on the basis of integumental organs and geographical distribution. Four biologically discrete populations are recognized, three being described as new species.

ACKNOWLEDGMENTS

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